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The Effect of Environmental Factors On the Abundance of Oak Regeneration Beneath Mature Oak Stands

BY
K. L. CARVELL
E. H. TRYON

MIXED OAK TYPES comprise approximately one-half of the forest area of West Virginia (Wray 1952). These include several distinct forest types of which the most widespread are: the yellow-poplar–white oak–northern red oak type of coves and lower slopes, the white oak–black oak–northern red oak type of fertile lower- and middle-third slopes, and the chestnut oak, white oak–chestnut oak, and scarlet oak types of dry upper-third slopes and ridges. Although many associates occur in these types, various species of oak predominate and constitute a valuable component. The percentage of oak must be maintained or increased, if the future productivity of these stands is to be assured.

The wide variation in the amount of oak regeneration beneath mature oak stands has attracted considerable attention. In some stands oak seedlings are conspicuously scarce (Fig. 1)—in others, dense thickets exist (Fig. 2). All conditions between these extremes occur. The deficiency of oak regeneration beneath mature oak stands is of grave concern to the forest manager since oak regeneration is virtually impossible to obtain quickly. Observa-

FIGURE 2. *A study plot having 55,750 oak seedlings per acre in the reproduction class. This stand had much more oak reproduction than any other area studied. The overstory is primarily white oak.*

FIGURE 1. *A study plot with 500 oak seedlings per acre in the reproduction class.*

The authors are Associate Silviculturist and Silviculturist, respectively, West Virginia University Agricultural Experiment Station. Published with the approval of the Director of the West Virginia University Agricultural Experiment Station as Scientific Paper No. 635. Manuscript received June 30, 1960.

tions of previously unmanaged oak stands, before and after cutting, emphasize that the composition of the next stand is largely predetermined by the composition of the understory at the time the overhead canopy is removed. A reservoir of oak seedlings and seedling-sprouts, built up over a period of many years, is the only real assurance that oak can be maintained after the harvest cutting. Where understory oaks are scarce or absent, a mixture of other, often less valuable, hardwoods will dominate the site even though natural regeneration methods which favor oaks are employed.

In order to determine which environmental factors influence the amount of oak regeneration beneath mature oak stands, a study was initiated in 1953 by foresters of the West Virginia Agricultural Experiment Station. This study included three distinct phases: (1) factors affecting acorn production and seedling establishment, (2) a study of density and composition of understories beneath mature oak stands, and (3) measurement of various site factors to determine their effect on seedling abundance. This paper summarizes the results of phase three.

Previous studies in the oak stands chosen for this experiment indicated that, although the number of oak seedlings varies greatly from one stand to another, their abundance is generally higher than expected when this study was initiated. In these stands total oak reproduction ranged from a minimum of 125 to a maximum of 55,750 per acre, and when first-year seedlings were excluded from 85 to 41,125 per acre (Tryon and Carvell (1958). Exluding oaks in their first growing season, it was found that one-half of the study areas had 2,500 oak seedlings or more per acre. The acorn production over a four-year period was essentially the same for each stand regardless of the abundance of oak regeneration. This suggests that differences in amount of oak regeneration are the result of site factors affecting the acorn after falling from the tree, or on the seedling itself.

White oak (*Quercus alba* L.) regeneration was more abundant than that of northern red oak (*Quercus rubra* L.), but the relationship between these two was closely related to the amount of white oak and red oak in the main crown canopy. Thus, the greater amount of white oak appeared to be related to the greater seed source. However, red oak, during the four-year period, was a more abundant seed producer than white oak. Comparison of the number of first-year seedlings in 1955 with the 1954 acorn crop indicated that for equal numbers of red and white oak acorns, five times as many white as red oak seedlings were established; therefore, white oak acorns were more effective in producing seedlings than red oak acorns (Tryon and Carvell 1958). Most of the seedlings, including oaks, were found in the smallest height class. Their abundance decreased rapidly with increasing height.

Oak regeneration was most abundant on the middle third of the slope, and on dry exposures (Carvell and Tryon 1959). Dry exposures on lower-third and upper-third positions were also well stocked with oak seedlings. Oak reproduction was least abundant on the moist sites where a characteristic cover of ferns and other vegetation carpeted the forest floor. On these sites herbaceous vegetation, shrubs, and tolerant tree seedlings shaded the forest floor so completely that oak seedlings were deprived of light during a critical period in establishment.

Review of Literature

Oak seedling establishment is best where the soil is loose since during germination the radicle cannot penetrate excessively compact surfaces (Korstian 1927). On compact soils the acorn is pushed around as the radicle attempts to penetrate, and eventually dries out. Thus, the humus layer is of great importance as it helps to maintain a loose, porous soil surface and affords mechanical support to the acorn as the radicle penetrates the soil.

Depth of litter influences seedling establishment by reducing water loss and equalizing temperature (Korstian 1927).

Studies of chestnut oak (*Quercus prinus* L.) showed that at least 1 inch of loose litter is needed for successful germination (Barrett 1939). Less than 1 inch or more than 2 inches of litter reduces survival. Minckler and Jensen (1959) also found that 1 inch of litter is desirable for establishment of oak seedlings, but concluded that thicker layers result in only slight reductions in the amount of oak regeneration.

White oak in the Piedmont of North Carolina was found to be relatively insensitive to moisture conditions in the top 12 inches of soil, when compared to shortleaf pine (*Pinus echinata* Mill.), sweetgum (*Liquidambar styraciflua* L.), and dogwood (*Cornus florida* L.). The long taproot which develops rapidly allows the oak seedling to obtain moisture from the deeper soil (Ferrell 1953).

Competing vegetation has a definite influence on seedling establishment and survival (Scholz 1955). Comparison of sites where bluegrass sod, woody shrubs, or dense ferns were the predominant cover, indicated that the lowest establishment occurred on the bluegrass sites and the highest on woody-shrub sites. Ultimately, however, the poorest survival resulted where competition from sensitive fern was severe. The greatest seedling losses occurred during July and August.

In studies of mixed oak stands in West Virginia and western Maryland Weitzman and Trimble (1957) found a strong correlation between site index and abundance of northern red oak regeneration. The greatest amount of red oak was found on site indices 50 and 60, and declined above and below these classes. The decrease was abrupt below site index 50 and gradual above site index 60. Barrett (1939) found that the germination percentage of acorns was higher on southern than northern exposures.

Procedure

A total of 59 plots was used in the study of environmental factors. These plots were located in Preston, Monongalia, Grant, Greenbrier, Mineral, Morgan, Randolph, and Tucker counties, West Virginia. The mixed oak stands selected for measurement were moderately well stocked and essentially even-aged, the result of heavy cuttings nearly a century ago. All stands were of sufficient age to produce considerable amounts of seed, the majority of the trees falling between 60 and 120 years of age. Stands which were being grazed or had been severely burned or heavily logged recently were not included in this study.

Reproduction was tallied on milacre quadrats. In each stand a red or white oak was selected as plot center. Regeneration was tallied in four quadrats beyond the crown and in four quadrats beneath the crown. Thus, a total of eight milacre quadrats were used, the most distant being 80 feet from the crown of the center tree. Regeneration included all stems less than 0.6 inch d.b.h. and was separated into height classes in the following manner: less than 1 foot, 1.0-1.9 feet, 2.0-2.9 feet, 3.0-3.9 feet, 4.0-4.9 feet, 5.0-5.9 feet, and 6.0 feet and larger. No distinction was made between seedlings, seedling-sprouts, and sprouts; however, all regeneration was of seedling or seedling-sprout origin.

The *history* of each study area was evaluated by a point system (Table 1). This assigned a numerical rating to each plot based on the degree of disturbance during the past 20 years. The greater and more frequent the disturbance, the higher the rating.

The *exposure* or *aspect* of each plot was determined with a hand compass. These were then rated numerically from 0 to 180. Since north- and east-facing slopes are moister and cooler than south- and west-facing slopes, northeast exposures were given a rating of zero. All exposures were rated on their departure from northeast. Thus, east and north slopes both received a rating of 45; southwest exposures were given a rating of 180.

Slope position was rated from 1 to 4,

depending on the position of the plot on the slope. Plots in bottoms and on lower-third slopes received a rating of 1; middle-third, 2; upper-third, 3; and ridges, 4.

Light intensity on the forest floor beneath each plot was measured with a photo electric cell. Measurements were taken at 16 randomly selected points within the plot. Their average was expressed as a percent of full sunlight in the open at the same time the plot measurements were taken.

Other site factors measured in this study included: soil texture, compactness of surface soil, depth of litter, percent slope, depth of A_1 soil horizon, and depth to mottling. Site index was determined by measuring age and height of three or more dominant or codominant white or northern red oaks on each plot.

Analysis of Data

In the initial stages of this analysis, graphs relating each environmental factor (independent variables) and abundance of oak regeneration (dependent variable) were constructed. These indicated that those factors directly responsible for variations in oak regeneration included history, exposure, percent sunlight, and slope position—and possibly combinations of these. Thus, in the initial phase of the statistical analysis a multiple regression was used of the form:

$$Y_t = b_0 + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4 + b_5x_5 + b_6x_6 + b_7x_7 + b_8x_8 + b_9x_9 + b_{10}x_{10} + b_{11}x_{11}$$

where Y_t = the total amount of oak regeneration on 8 mil-acre plots

x_1 = exposure

x_2 = slope position

x_3 = percent sunlight

x_4 = exposure × slope position

x_5 = slope position × percent sunlight

x_6 = exposure × percent sunlight

x_7 = exposure × slope position × percent sunlight

TABLE 1. Evaluation of history by point system.

Environmental disturbance	Points
Grazing	
Over ten years ago	0
Five to ten years ago	
Light	1
Heavy	2
Less than five years ago	
Light	2
Heavy	3
Fire	
No fire within past 15 years	0
Ground fire within past 15 years	2
Logging operations	
No logging within past 20 years	0
Ten to 20 years ago	
Light	1
Heavy	2
Five to ten years ago	
Light	2
Heavy	3
Less than five years ago	
Light	3
Heavy	4

x_8 = history

x_9 = slope position × history

x_{10} = exposure × history

x_{11} = exposure × percent sunlight × history

$b_0, b_1, b_2 \ldots, b_{11}$ = numerical coefficients to be obtained from the data

The normal equations of the regression were determined and the forward solutions and mean square of the residuals obtained. The forward solution was then recalculated using the Kincer and Mattice method (Kincer and Mattice 1928) for determining the most significant factors. In this analysis only one variable, history (x_8), was significant (1 percent level). The remaining independent variables were not significant when the effect of history had been removed.

Similarly, this regression was recalculated substituting Y_1 (oaks over 1 foot in height) for Y_t. In this analysis x_8 (his-

tory) was also the only significant variable (1 percent level). The remaining independent variables were not significant after the effect of history had been removed.

The Kincer and Mattice tests suggested that many of the other variables would show a significant relationship with the amount of oak regeneration (Y), if the effect of history had not been removed initially. It was considered important that these be analyzed in order to help explain the role of history. Thus, 22 separate regressions were calculated of the form:

$$Y_t \text{ or } _1 = b_0 + b_n x_n$$

where Y_t = the total amount of oak regeneration on 8 milacre plots

Y_1 = the number of oak seedlings over 1 foot in height on 8 milacre plots

x_n = each of the independent variable from x_1 through x_{11}

b_0, b_n = numerical coefficients to be obtained from the data.

The results of these regressions are shown in Table 2. These F values demonstrate that many variables. but primarily those which include history, are strongly related to both total oak regeneration and number of oaks over 1 foot in height. Next in importance to history (x_8) and those variables which include history (x_9, x_{10}, and x_{11}), are percent sunlight (x_3) and the even more significant interaction between percent sunlight and exposure (x_6).

TABLE 2. F values for independent variables. F values must exceed 4.01 for significance at the 5 percent level; and 7.10 for significance at the 1 percent level.

Independent variables	*F* values: Oak over 1 Foot	*F* values: Total oak
x_1 Exposure	2.79	1.63
x_2 Slope position	0.05	0.01
x_3 Percent sunlight	16.77**	12.33**
x_4 Exposure x slope position	1.07	0.94
x_5 Percent sunlight x slope position	8.80**	9.95**
x_6 Exposure x percent sunlight	19.79**	13.32**
x_7 Exposure x slope position x percent sunlight	12.71**	12.50**
x_8 History	37.23**	21.61**
x_9 History x slope position	24.18**	18.57**
x_{10} History x exposure	31.96**	16.98**
x_{11} History x percent sunlight x exposure	31.67**	14.44**

**Significant at the 1 percent level.

Back solutions and coefficients for the significant variables were computed. These are presented on a per acre basis in Table 3. The graphs for the more important of these are shown in Figures 3, 4, and 5.

Discussion

The F values in Table 2 indicate a much closer correlation, in nearly all instances, between the significant variables and oak

TABLE 3. Regression equations for all significant variables. Y values are expressed on a per acre basis.

Independent Variables	Oaks over 1 foot	Total oaks
x_3	$Y_1 = -346.12 + 533.05\ x_3$	$Y_t = 2{,}692.17 + 663.75\ x_3$
x_5	$Y_1 = 643.19 + 127.28\ x_5$	$Y_t = 3{,}416.29 + 188.36\ x_5$
x_6	$Y_1 = 336.16 + 3.63\ x_6$	$Y_t = 3{,}633.79 + 4.37\ x_6$
x_8	$Y_1 = -2{,}815.64 + 2{,}424.62\ x_8$	$Y_t = 27.78 + 2{,}838.13\ x_8$
x_9	$Y_1 = -1{,}623.32 + 706.74\ x_9$	$Y_t = 605.96 + 902.24\ x_9$
x_{10}	$Y_1 = -908.50 + 13.74\ x_{10}$	$Y_t = 2{,}431.85 + 15.44\ x_{10}$
x_{11}	$Y_1 = 1{,}150.03 + 0.71\ x_{11}$	$Y_t = 4{,}852.25 + 0.75\ x_{11}$

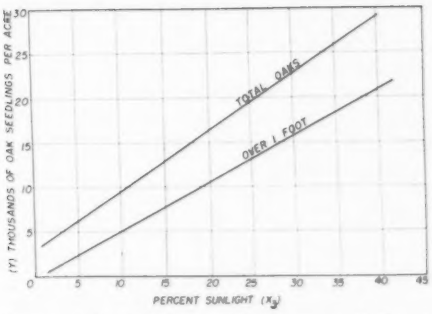

FIGURE 3. *Relation of percent sunlight to total oak regeneration and oak regeneration over 1 foot in height (per acre).*

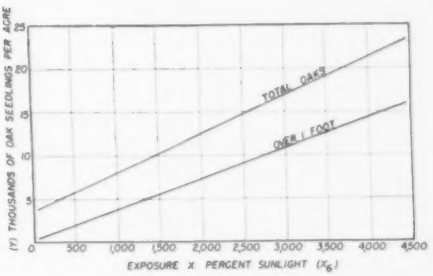

FIGURE 4. *Relationship of exposure x percent sunlight to total oak regeneration and oaks 1 foot in height (per acre).*

regeneration over 1 foot (Y_1) than with total oaks (Y_t). This suggests that the ability of oak regeneration to persist on a specific site is more closely related to environmental conditions than is its ability to become established.

Stand history (x_8), or amount and degree of disturbance, shows the closest correlation of any independent variable with both total oak regeneration (Y_t) and amount over 1 foot (Y_1). Since the regression equations for history both have positive slope coefficients (Table 3), this indicates that the greater the past disturbance, the more oak regeneration. The increase in oak seedlings, particularly those over 1 foot in height, is probably due to the regular opening up of the crown canopy through logging or surface fires, allowing increased sunlight to reach the forest floor, or the reduction in competing vegetation through grazing because of the low palatability rating of oak compared with most associated trees and shrubs. Stands which have been disturbed repeatedly, thus producing openings in the main crown canopy at regular intervals, should maintain a large number of oak seedlings and seedling-sprouts over 1 foot in height.

The significance of percent sunlight (x_3) likewise suggests that lack of light is largely responsible for the reduction in number of oak seedlings particularly those over 1 foot in height. This can be explained by the increasing intolerance to shade of oak seedlings as they develop. When the effect of sunlight is combined with exposure (x_6), an even closer correlation is obtained. This suggests that oak seedlings can persist not only in the more open stands typical of dry exposures, but can be brought in and maintained on the moister exposures, if adequate sunlight reaches the forest floor.

The lack of a linear relationship between oak regeneration and slope position (x_2), and the decrease in correlation with exposure (x_4) or history (x_9) when slope position is included, indicates that oak regeneration does not increase as the upper

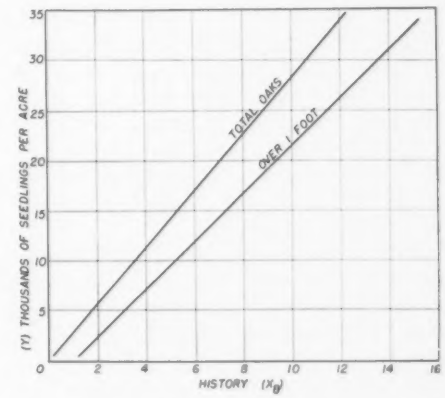

FIGURE 5. *Relation of history to total oak regeneration and oaks over 1 foot in height (per acre).*

slopes and ridges are approached. A previous study (Carvell and Tryon 1959) indicated that oak regeneration was more abundant on the middle-third slope position, and that oak regeneration was more abundant on those sites with dry exposures. Even though dry exposures on lower-third and upper-third positions were well stocked with oak seedlings, they did not compare with middle-third slopes. Thus, although oak seedlings develop a taproot during their first year, this is possibly inadequate to cope with the limited moisture conditions on upper slopes and ridges, and many seedlings do not survive in spite of the increased sunlight usually available on the forest floor of these sites. The slow growth and adverse conditions for all species on these sites, however, allow oak to perpetuate itself in spite of its reduced reproductive capacity.

The significance of x_6 (exposure $\times$ percent sunlight) defines the sites on which oak can be perpetuated with ease, and those on which particular care must be taken to obtain an adequate number of seedlings by the end of the rotation. The drier exposures, those with ratings 90 through 180, or southeast, south, west, and northwest slopes, are typical oak sites. Here, oak types form the climax or long-range subclimax, and will perpetuate themselves more readily than on the moister exposures. On moister exposures the increased competition from herbaceous vegetation, shrubs, and more tolerant tree species, the denser overhead canopy, and the resulting greater competition for light, would require regular crown openings to maintain the vigor of new oak seedlings and to build up the desirable reservoir which assures abundant oaks in the next rotation.

The lack of any relationship between depth of litter and amount of oak regeneration is attributed to the narrow range of litter depths encountered in these stands.

Summary

The scarcity of oak regeneration beneath previously unmanaged, mature oak stands is of grave concern to the forest manager, since oak reproduction cannot be obtained quickly, and the composition of the new stand is largely predetermined by the composition of the understory at the time the overhead canopy is removed. To determine those environmental factors which are responsible for this lack of regeneration beneath many mature oak stands, 59 study areas were established and various environmental factors measured.

This analysis indicates that the ability of oak regeneration to persist on a specific site is more closely related to environmental conditions than is its ability to become established.

The percent sunlight reaching the forest floor shows a significant positive correlation with the amount of oak regeneration. The regression equation relating oak regeneration to percent sunlight indicates that the greater the percent of sunlight, the larger the number of oak seedlings. When percent sunlight is combined with exposure (percent sunlight $\times$ exposure) an even closer correlation is obtained. This suggests that oak seedlings can persist not only in the more open stands, typical of dry exposures, but can be brought in and maintained on moist exposures where regular thinnings have been used to provide adequate light.

Stand history or degree of disturbance during the past 20 years was found to be very closely correlated with the amount of oak regeneration. Stands which have been thinned, grazed or lightly burned during the past two decades generally possess a greater reservoir of oak regeneration than undisturbed stands. This increase is attributed to the continuous supply of light which reaches the forest floor because of these repeated disturbances.

The abundance of oak regeneration shows no direct correlation with increasing slope position, i.e. from bottom to ridgetop. Previous studies on these plots had indicated that the largest number of oaks occurred on the middle-third slope positions, and decreased on the upper-third slopes and ridges. These results were substantiated by this analysis.

On the drier exposures (southeastern, southern, southwestern, western, and northwestern) oaks can be maintained with little difficulty since here oak types form the climax or long-range subclimax. On moister exposures, however, if a reservoir of oak regeneration is to be built up before the end of the rotation, care must be used to provide regular crown openings. A series of thinnings during the last years of the rotation is suggested to provide sufficient sunlight for seedling establishment and survival.

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The Effect of Site and Other Factors On Specific Gravity and Bending Strength Of California Red Fir

BY
ARNO P. SCHNIEWIND

THE RELATIONSHIP between conditions of growth and wood properties has attracted considerable attention over the years. Numerous experimental investigations have been made with varied and often contradictory results. Because of the multitude of possible growth factors responsible for variations in wood properties this is not surprising, especially since it is but rarely practicable to include more than a few of these factors in a given investigation.

The literature on the effect of site on specific gravity and hence other wood properties, reviewed in detail by several authors (Spurr and Hsiung 1954, Trendelenburg and Mayer-Wegelin 1955, and Larson 1957), contains many conflicting reports. Recently Klauditz and Stolley (1957) found that for Douglas-fir grown in Germany, differences in density due to site were indicated but not clearly shown by the work done, whereas a more extensive study on the same species of similar origin (Knigge 1958) showed no influence of site on the physical and mechanical properties of the wood but a tendency for specific gravity to decrease with changes in geographic location from east to west. Göhre (1958) examined specific gravity data of his own and from the literature by means of statistical methods, and concluded that differences between sites and geographic locations were small compared with the variation within a site, i.e., between individual trees. His conclusion was challenged by Stojanoff and Entcheff (1958) but the same views were reaffirmed by Göhre and Götze (1958). Jayne (1958) found a very definite influence of site on the specific gravity of plantation-grown red pine—the poorer site producing wood of higher specific gravity—and suggested the study of individual factors rather than of the total site complex.

The variation in specific gravity according to height and radial position within the tree has been studied by many investigators and reference is made again to the reviews cited previously. The effect of height can be evaluated readily, but not radial position at a given height, because of a confounding of ring width, age, and horizontal position (a functional variation related to the ability of the stem to resist bending moments). Although the effect of ring width and age can be separated statistically, some meaningful quantitative expression for horizontal position in terms of its function would be required before it can be treated as a separate factor.

The effect of ring width on specific

The author is Assistant Wood Technologist, Forest Products Laboratory, University of California.

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gravity is of particular interest to foresters in connection with the management of second-growth and plantation timber. Many authors have discounted ring width as a primary factor and have demonstrated age as being the more important of the two. Results of the most recent investigations range from a clear effect of age and a minor effect of ring width (Rendle and Phillips 1958), and a highly significant effect of both ring width and age (Fry and Chalk 1957) to a lack of a definite age effect determined qualitatively (Aldridge and Hudson 1958, 1959) and by statistical exclusion of the effect of ring width (Knigge 1958). The evidence in regard to the effect of age on specific gravity is therefore not clear.

There is no question that the literature on the effect of growth conditions on specific gravity shows far greater general agreement than the foregoing discussion indicates. On the other hand, the conflicting opinions regarding such important factors as site, ring width, and age indicate the need for much additional work in this area of study.

Objectives

The present study was designed primarily to answer a specific question. This arose when a large mill cutting California red fir (*Abies magnifica* A. Murr.) experienced difficulties in sawing the lumber on the headrig. Some of the lumber was extremely rough, caused by a tearing of the springwood so severe that standard allowances for dressing the lumber were insufficient. It was noted that this occurred only in the heartwood, primarily in the interior of fast-grown trees, and was associated with extremely low weight of the boards. A study attempting to relate this defect to timber site was made by the mill. Three topographic sites were studied and were defined as follows:

Slope site—Gentle slope, well-drained site, good timber form

Ridge-top site — Ridge tops, shallow soil, trees shorter, smaller, limby

Meadow site — Meadows, poorly drained site, edge-type timber

where the slope site and ridge-top site represent the extremes in edaphic factors for the development of the tree (Hallin 1957). It was found that less than 1 percent of the lumber from ridge tops showed serious springwood tearing (more than $\frac{1}{8}$-inch deep), whereas these percentages were 7.8 and 34.3 for lumber from meadows and slopes, respectively. Lumber from ridge-top trees appeared to be heavier and was generally more slowly grown than that from the other sites, but much of the ridge-top lumber with growth rings as wide as or wider than defective lumber from the other areas was also resistant to the springwood tearing. It was felt that the tearing of the springwood could be remedied by changes in the sawing technique, but the question arose whether the tearing and light weight which appeared to be related to site were also associated with abnormally low strength of the lumber. The major objective of the present investigation was therefore to determine the influence of site on the strength properties (specifically, the flexural strength) of California red fir.

Further objectives were to determine the influence of specific gravity, growth rate, latewood percentage, and age[1] on both modulus of rupture and modulus of elasticity in flexure.

Procedure

The experimental work was done on material from 12 trees from each of the three sites. The trees were selected within the Golden Summit area near Stirling City, California. Each of the three sites was, in a sense, replicated, i.e., for a given site, trees were selected from several plots which were not contiguous but which conformed to the definition of that site. Practical reasons prevented equal numbers of plots and trees per plot. The number of plots ranged from five to six per site with

[1]The term age, as applied to specimen material, is used in the sense of number of rings from the pith and represents the age of the cambium at the time the wood in question was formed.

a maximum of four trees per plot. After the sample trees had been selected, marked, and described they were felled and the logs brought to the mill at Stirling City as part of a regular logging operation.

With the exception of two codominant trees all of the trees were dominants and came from an altitude ranging from 6,000 to 6,600 feet. Stand density within a site varied from plot to plot, with a tendency toward higher density on the slope sites than on the ridge top and meadow sites. The trees from slopes showed the greatest vigor, followed by those from meadows, and finally those from ridge tops. Some data characterizing the trees from the three sites are given in Table 1.

Because a large variation in properties was expected as a result of position within the tree, it was decided to include radial position as a factor and to keep vertical position constant. The test material was taken from the second 16-foot log (to avoid problems associated with the sweep commonly found in butt logs of this species). A cant, 3-inches thick and extending through the pith from bark to bark, was sawn from each of the sample logs. The cants were divided into three equal parts with respect to radial position, namely, interior (near the pith), intermediate, and outer (near the bark) positions. Two duplicate specimens were taken from each position.

The experimental design employed lends itself to a mixed-model analysis of variance, with site and position as the fixed variables and trees as the random variables, with two duplicates of each position.

It was originally intended to make the flexural tests on the standard 2 × 2 × 30-inch specimens, but because of spiral grain and numerous knots, particularly in the interior position, the specimen size had to be reduced to 1 × 1 × 16-inch. The tests were made in the green condition according to standard procedure, secondary method (American Society for Testing Materials 1955). Modulus of rupture and modulus of elasticity were determined for each specimen. After each test, two sections were removed from the specimen near the area of failure. One of these was used to determine specific gravity (based on oven-dry weight and green volume) by the water immersion method. The other section was used to determine ring width, latewood percentage, and age.

The average ring width and latewood percentage of each specimen were obtained by measuring microscopically to 0.001 inch the width of the latewood band and the total width of each full ring found in the section. The latewood definition of Wiksten (1944) was used. Age determinations had to be confined to the sample material available, the central cant from the second 16-foot log, and are therefore based on a point 16 feet above the stump.

The average age of each specimen (in the sense of number of rings from the pith) was determined by matching its cross section (representing 1-inch of radius) to the cross section of the blank it was cut from (representing 2½ inches of radius and 30 inches of length) followed by matching of the larger section to the full cross section cut from the lower end of each cant. In this manner the specimen cross section was located in the full cross section and a ring count could be made. The principles of dendrochronology were employed in matching sections and in most cases positive determinations could be made. In some cases there was some uncertainty about the age determination of material from the interior position, because the rings in that position tended to be uniformly wide and were probably affected more than the other positions by variations in width

TABLE 1. Age and size of trees from three sites.

	Slopes	Ridge tops	Meadows
Age at 16 ft. above stump, years	144[1]	159	142
D.b.h., inches	39	37	46
Height, feet	130	90	120

[1]Each figure is an average based on 12 trees.

with height along the 16-foot length of the sample material. The average age of each specimen gives the number of years which have passed between the time the tree reached a height of 16 feet above the stump and the time the wood located in the center of the specimen cross section was formed.

Results and Discussion

The data summarized in Table 2 show all of the property values by site and radial position within the tree. The age of the material from the different sites does not differ greatly at comparable radial positions. The lower age of the material from meadows reflects its greater ring width, particularly at the inner positions. The ring width, as might be expected, decreases from pith to bark in each site. Very little variation is found in latewood percentages, which seems particularly unaffected by radial position.

Examination of the data for modulus of rupture, modulus of elasticity, and specific gravity (Table 2) shows only minor differences between sites. Position, on the other hand, appears to have a more pronounced effect. With the exception of the specific gravity values for ridge-top material, property values increase as position is shifted from pith to bark. The specific gravity data from the ridge tops show a maximum at the intermediate position which is reflected in the modulus of rupture data but not in the modulus of elasticity data. Surprising is the relatively high specific gravity in the interior position of the ridge-top material, which is higher than the corresponding values for the other sites, while no such differences are apparent for the modulus of elasticity and modulus of rupture data.

The data for modulus of rupture, modulus of elasticity, and specific gravity were subjected to analyses of variance. Two types of analyses were made for each of these three properties. The first type was a mixed-model analysis of variance with radial position and site as the fixed variables and trees as the random variable. This was used to determine the effect of site and the overall effect of radial position on property values. The second type was a two-factor

TABLE 2. Summary of flexure test results and associated measurements.

Property	Position	Slopes	Ridge tops	Meadows
Age, based on 16 ft. above stump, years	Interior	36[1]	40	30
	Intermediate	64	70	61
	Outer	106	107	102
Ring width, inches	Interior	0.151	0.136	0.194
	Intermediate	0.094	0.098	0.133
	Outer	0.069	0.066	0.081
Latewood percentage	Interior	14.3	13.2	14.8
	Intermediate	14.8	13.7	15.8
	Outer	14.2	12.2	14.4
Modulus of rupture, psi	Interior	5,200	5,270	5,180
	Intermediate	5,720	5,640	5,520
	Outer	5,800	5,630	5,590
Modulus of elasticity, 1000 psi	Interior	1,020	980	980
	Intermediate	1,230	1,100	1,170
	Outer	1,300	1,170	1,230
Specific gravity	Interior	0.307	0.321	0.309
	Intermediate	0.324	0.329	0.315
	Outer	0.327	0.322	0.321

[1]Each figure is an average of 24 observations and is based on data from 12 trees.

TABLE 3. Summary of results of analyses of variance by individual sites.

Property	Factor	Slopes	Ridge tops	Meadows
Modulus of rupture	Trees	**	*	**
	Position	**	**	**
	Trees × position	**	----[1]	**
Modulus of elasticity	Trees	*	*	**
	Position	**	**	**
	Trees × position	----	----	**
Specific gravity	Trees	**	ns	**
	Position	**	ns	**
	Trees × position	**	----	**

**Significant at 1 percent level; *significant at 5 percent level; ns = not significant.
[1]Interaction term used to test effect of trees and position.

analysis of variance with radial position and trees as the variables. This was applied separately to the data from each site and used to investigate the effect of trees, radial position, and their interaction.

The effect of site on modulus of rupture, modulus of elasticity, and specific gravity, as tested against the effect of trees, was not statistically significant. In other words, the variation in property values from tree to tree within a given site was as great as or greater than variations from site to site. The overall effect of radial position, as tested against the interaction term of trees and radial position, was highly significant (at the 1 percent level) for modulus of rupture and modulus of elasticity, but not for specific gravity.

The results of the remaining analyses of variance are summarized in Table 3. As may be seen from this table, trees had a significant effect on property values except on specific gravity in the ridge top site. In other words, property values, except as noted, differed from tree to tree when the effect of radial position was taken into account. The same results, with the same exception, were obtained for the effect of radial position. This shows a significant increase in property values from pith to bark. The interaction between trees and radial position is highly significant (at the 1 percent level) in all cases where it could be investigated. This indicates that the steepness of the gradient of property values from pith to bark varies significantly from tree to tree. In several cases (Table 3) complications arose because of lack of homogeneity of variances, i.e., the variance of material from the interior position was significantly greater than that of the material from the other positions. Therefore the interaction term rather than the error term was used to test the effect of trees and radial position, and suitable adjustments (Box 1954) had to be made in these cases.

The effect of radial position was studied in more detail by comparing pairs of means from the three positions within each site. The studentized range (Dixon and Massey 1951) was used to test the significance of differences between means. The results are summarized in Table 4. For the modulus of rupture and modulus of elasticity data an identical pattern was obtained in all three sites. The results show that the flexural property values increase significantly from the interior to the intermediate position, but that from there on no further significant increase takes place. The specific gravity data from slopes show the same pattern, those from the ridge tops exhibit no significant difference between any of the means, and those from the meadows only a significant difference between the interior and the outer position, indicating a more gradual increase of specific gravity from pith to bark in this case. Thus, although there is no overall effect of

TABLE 4. Comparison of the means from radial positions for each site.

Property	Positions	Slopes	Ridge tops	Meadows
Modulus of rupture	Interior vs. intermediate	**	**	**
	Interior vs. outer	**	**	**
	Intermediate vs. outer	ns	ns	ns
Modulus of elasticity	Interior vs. intermediate	**	**	**
	Interior vs. outer	**	**	**
	Intermediate vs. outer	ns	ns	ns
Specific gravity	Interior vs. intermediate	**	ns	ns
	Interior vs. outer	**	ns	**
	Intermediate vs. outer	ns	ns	ns

**Significant at 1 percent level; ns = not significant.

site on specific gravity, the pattern of variation with radial position does vary from site to site. However, this is not reflected in the distribution of flexural property values.

Site conditions as included in this study could not be shown to have a significant effect on modulus of rupture, modulus of elasticity, and specific gravity, when compared with the differences found from tree to tree. These findings agree with the conclusions of Göhre (1958). However, comparison of the grand averages of this study with published data (Forest Products Laboratory 1955) shows that the present data gave lower average values particularly for modulus of rupture:

	Present study	*Previously published*[2]
Modulus of rupture	5,510 psi	6,000 psi
Modulus of elasticity	1,130,000 psi	1,210,000 psi
Specific gravity	0.319	0.37

The highest specific gravity observed on a single specimen from this study was 0.389. In a study by Dohr[3] four out of 12 trees tested (covering a wider geographic range than the present study) had an average specific gravity greater than 0.389. It would therefore seem that the results of this study might not be valid when the entire population of California red fir trees is considered, either because the differences between the site conditions investigated were not great enough or possibly because of genetic variation on a regional basis.

The difficulties in sawing were found to be related to site, but no such relationship was found in this study between site and flexural property values, and site and specific gravity. Thus it would appear that the tearing during sawing is not indicative of low strength. Since the material from the ridge tops was found to be particularly resistant to tearing, and the tearing was observed to be predominant in the interior of the heartwood, the relatively uniform density gradient of the ridge-top material indicates that specific gravity is the important factor. Site might therefore have an effect on specific gravity in the interior position only. This would be expected to lead to a significant interaction of site and position but this point could not be tested directly. However, such an effect is indicated by the fact that significant differences between positions were found in only two of the three sites.

It is of great interest that modulus of rupture and modulus of elasticity in the

[2]These values were obtained on 2 × 2-inch specimens. However, the difference in size is not sufficient to invalidate comparisons with the results of this study.

[3]The mechanical properties of California red fir (*Abies magnifica*) by A. W. Dohr, U. S. Forest Prod. Lab., Madison, Wis., unpublished report, circa 1952.

ridge-top site show patterns of variation with position which are not consistent with the radial specific gravity pattern. The specific gravity maximum in the intermediate position is reflected only in the modulus of rupture data and there but slightly. As the previous analysis showed, both moduli are affected significantly by position, which was not the case with the specific gravity of this site.

Although specific gravity is generally considered to be an excellent indicator of the strength properties of wood, exceptions have been noted. Kraemer (1950), in a study of red pine, found that within sites specific gravity does not have a significant effect on flexural strength. A later study on the same material (Kraemer 1951) showed that when fibril angle, rings per inch, and specific gravity are considered, the effect of the last factor on flexural strength is negligible. Of even greater interest in this connection is the observation of Littleford (1958) that specific gravity differences from an inner to an outer growth zone in Douglas-fir did not fully explain corresponding differences in modulus of rupture.

Since an effect of site was found to be wanting and since position can be expressed more readily in terms of age and ring width (neglecting any purely functional position factor which might exist), the entire data could be subjected to a series of multiple regression analyses. The factors involved, in various combinations, were modulus of rupture, modulus of elasticity, specific gravity, age, ring width, and latewood percentage.

Five separate multiple regression analyses were made: (1) specific gravity as a function of age, ring width, and latewood percentage, including all of the data; (2) the same variables as under 1 but including only the data from the interior position; (3) the same variables again but including only the data from the intermediate and outer positions; (4) modulus of rupture as a function of specific gravity, age, ring width, and latewood percentage; and (5) modulus of elasticity as a function of specific gravity, age, ring width, and latewood percentage. The specific gravity data were divided according to growth zones. This was done to ascertain whether in the interior growth zone, the relationships between specific gravity and the other factors differed appreciably because of the possible inclusion of juvenile wood. The regression statistics are summarized in Table 5.

Of particular significance is the fact that the regression coefficients for age are in no case significantly different from zero. There might be objection to this finding on the basis that more direct age determinations might have led to different results. However, the coefficients are of such low magnitude that within the range of age values encountered, the effect on the mag-

TABLE 5. Terms of the regression equations and multiple correlation coefficients (R).

	Dependent variables				
	Specific gravity				
	All data	Interior only	Intermediate and outer only	Modulus of rupture	Modulus of elasticity
Constant term	0.316	0.294	0.316	6.48×10^3	3.241×10^5
Regression coefficients:					
Specific gravity				$1.537 \times 10^{4**}$	$2.606 \times 10^{6**}$
Age	$-3.61 \times \overline{10}^{6}$ ns	$4.15 \times \overline{10}^{4}$ ns	$-1.16 \times \overline{10}^{5}$ ns	−0.3244 ns	$3.941 \times 10^{2**}$
Ring width	−0.187**	−0.108 ns	−0.219**	$-2.579 \times 10^{3**}$	$-1.381 \times 10^{6**}$
Summerwood %	$1.764 \times \overline{10}^{3**}$	$1.509 \times \overline{10}^{3*}$	$1.918 \times \overline{10}^{3**}$	$1.875 \times 10^{1**}$	$7.392 \times 10^{3**}$
R	0.506	0.505	0.486	0.870	0.735

*Significant at 5 percent level; **Significant at 0.1 percent level; ns = not significant.

nitude of the dependent variable is very small. In addition, the coefficients for age are positive in some cases and negative in others.

As pointed out earlier, age determinations were most uncertain in the interior position, and it is of interest to note that where the data were separated according to position, the probability of falsely rejecting the null hypothesis (i.e., age has no significant effect on specific gravity) differed considerably. In the case of the data from the interior position, the level of probability is 20 percent; considering the data only from the intermediate and outer positions the level is 90 percent. In other words, the data from positions away from the pith, where the age could be determined with greatest precision, showed the least likelihood of a significant age effect. These considerations suggest that although there is no significant effect of age on specific gravity nor on modulus of rupture and modulus of elasticity over the entire cross section of the tree, age might be a significant factor in the very early stages of growth.

Further examination of the regression statistics which contain specific gravity as the dependent variable shows additional differences between the data from the interior and those from the combined intermediate and outer positions. Ring width is highly significant (0.1 percent level of probability) when the entire data and those from the intermediate and outer positions are included but is not significant when the data only from the interior position are considered. Similarly, the level of significance for the effect of latewood percentage is changed from 0.1 to 5 percent when the data from the interior position are singled out. It is surprising that ring width is not significant in the interior position, and that latewood percentage is the only significant factor in this case.

All of the factors investigated except age have a highly significant effect on both modulus of rupture and modulus of elasticity. Most of the variation in values for modulus of rupture and modulus of elasticity can be attributed to variations in specific gravity. The simple correlation coefficient for modulus of rupture and specific gravity is 0.835; the multiple correlation coefficient is 0.870. The inclusion of factors other than specific gravity therefore increased the variation in modulus of rupture which could be explained[4] by only 6 percent. In the case of the modulus of elasticity data the improvement is more substantial. The simple correlation coefficient here is 0.590 compared with a multiple correlation coefficient of 0.735, equivalent to a 19 percent increase in variation that can be explained.

Where specific gravity is the dependent variable, the multiple correlation coefficients are low in each case. The greatest single correlation coefficients are for specific gravity and ring width (−0.373) for all data, specific gravity and age (0.414) for data from the interior position only, and for specific gravity and latewood percentage for the combined data from the intermediate and outer positions (0.332). The increase in variation that can be explained ranges from 8 to 13 percent.

It may be noted that the three analyses including data from all positions were made using alternately ring width and rings per inch as one of the independent variables. In each case the use of ring width over its inverse increased the multiple correlation coefficient. This was most pronounced where modulus of elasticity is the dependent variable. There the coefficient was increased from 0.672, using rings per inch, to 0.735, using ring width. This indicates that the relationships between ring width and the dependent property values are more nearly linear—as required by the regression model used in this study—than the relationships where rings per inch is used.

None of the results of the regression analyses is without precedent. This in-

[4]The percentage of variation of the dependent variable which can be explained by the variation of the independent variables is equal to 100 times the squared multiple correlation coefficient.

cludes the observed effect of latewood percentage on specific gravity, but the effect of latewood percentage independent of specific gravity on both modulus of rupture and modulus of elasticity is somewhat surprising. This is particularly so in view of the gradual transition and lack of contrast between earlywood and latewood, as well as the fact that the observed latewood percentages were relatively low ranging from 4.8 percent to 28.8 percent (cf. Table 2 for relative uniformity). Specific comparisons cannot be made because no other applicable data appear to be available for California red fir. Comparison with other species, except in general terms, does not seem to be justified.

Although the results of this study contribute to our knowledge of specific gravity and flexural property variations, the conflicts regarding the effect of such factors as ring width and site have not been touched upon and remain unresolved. What seems to be needed here is an entirely new and comprehensive approach. Provided that all of the possible major factors can be expressed numerically, the imaginative use of electronic computers in making multiple regression analyses, which can now be extended to 33 independent variables (Black 1959), may prove to be highly profitable and enlightening.

Summary of Conclusions

1. Site has no significant overall effect on specific gravity, modulus of rupture, or modulus of elasticity, but the radial distribution of specific gravity values differs from site to site.

2. Within each of the three sites investigated, both trees and radial position within trees significantly affected specific gravity, modulus of rupture and modulus of elasticity. An exception was the specific gravity for ridge tops.

3. Age has no significant effect on specific gravity, modulus of rupture, or modulus of elasticity when ring width, latewood percentage and—where the flexural properties are concerned—specific gravity are held constant. However, age may have an indirect effect by influencing one of the other factors, such as ring width.

4. Ring width and latewood percentage have significant effect on specific gravity; and ring width, latewood percentage, and specific gravity have a significant effect on modulus of rupture, and modulus of elasticity. An exception to this was found when only the specific gravity data from the interior position as a function of age, ring width, and latewood percentage were considered. In this case only latewood percentage had a significant effect on specific gravity.

5. Use of ring width instead of rings per inch as a variable improved the estimate of specific gravity, modulus of rupture, and modulus of elasticity.

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Some Considerations on the Statistical Design for Provenance and Progeny Tests In Tree Improvement Programs

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FOREST TREES differ considerably from most agricultural plant crops in many aspects. Consequently statistical designs for field tests developed for the improvement of agricultural crops may not, in some cases, be validly applied to forest trees without modification. To recognize the basic differences between forest trees and agricultural crops, to modify the present available statistical designs, and even to develop some special methods in order to accomplish the objectives of tree improvement, is a complicated task and requires mutual efforts by tree breeders and statisticians. This paper discusses some special statistical considerations in designing a provenance or progeny test for forest trees.

Some Basic Differences Between Agricultural Crop Plants and Forest Trees

Following are several important fundamental differences that exist between most agricultural plants and forest trees. Some of these differences profoundly influence the improvement methods employed, especially as they relate to progeny and provenance tests.

1. Forest trees, with the possible exception of certain horticultural crop plants, usually live longer and mature later as compared with most agricultural crops. Consequently, tests relating to the yield of forest trees require: (a) at least a commercial rotation which, for certain products, may be a period of many years; (b) a careful initial planning, since any subsequent changes may be impossible or too costly; and (c) great caution against any mishaps, especially in the early stages, because the effects of such mishaps may possibly be accumulated and tend to conceal the true results of the test. Although a sequence of crosses can theoretically be carried out on forest trees, it may take a prohibitively long time to complete the evaluation. Therefore, the F_1 is most commonly used to test the cross at the present time. Since mass multiplication of certain genetically superior individuals is slow in spite of the fact that crosses can be repeated on the same individuals every year, techniques relating to the vegetative propagation of forest trees may play an important role in tree improvement programs.

2. Due to heterozygosity, the variation of individuals within a given provenance or progeny of forest trees is relatively large. The position effect due to soil heterogeneity is not the only experimental error to be considered. In evaluating a provenance or progeny of forest trees, attention must not

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only be directed to the mean but also the variance. Uniformity within a progeny is one of the criteria for selecting superior materials in most crop breeding programs; but this is not true in the case of tree improvement, especially for species whose primary products are sawlogs and veneer logs. It does not necessarily follow that provenances with small variance are more desirable than those with larger variance, assuming their means to be the same. On the contrary, provenances with large variance are preferred if their mean values are favorable. This is due to the fact that the number of final crop trees of a forest is only a small fraction of the initial number of trees planted. During the course of development of a stand, many trees are lost through natural and artificial thinnings. Given an acceptable mean value, provenances or progenies with larger variance will consist of some extremely good and poor individuals. The poor ones will act as "trainers" and will ultimately be eliminated through thinnings. Thus the final harvest in such stands will be composed of better crop trees than in those stands grown from provenances with the same mean value but smaller variance. However, to insure good spatial distribution of crop trees, the number of good trees planted must be greater than those harvested.

3. Although yield differences as low as 5 percent of the mean may be of theoretical interest to the tree breeder, it is usually not economically feasible to make such elegant distinctions. The following considerations have influenced tree breeders to look for larger differences: (a) heterogeneity within progenies and wide soil variability of testing sites make tests designed to detect small differences in yield too costly; and (b) since test results are subjected to changes of location and time when applied, progenies with a yield superiority of only 5 percent of the mean cannot be relied upon to maintain such superiority when planted on other sites in other years.

If differences in yield of more than 5 percent of the mean do not exist, it is suggested that the improvement work be directed to other characteristics.

Size of Plot

Since an individual forest tree can be considered as an experimental unit and the spacing between trees for certain species at the time of establishment is arbitrarily fixed, the size of plot used for provenance or progeny test may be expressed in the number of trees per plot ranging from one as high as more than one hundred. Following Smith's study (1938), Wright and Freeland (1959) found that the single-tree plot is more efficient than the multiple-tree plot for red pine and other species, hence they suggested that the single-tree plot should be used for provenance or progeny tests.

This conclusion is true only if the following assumptions have been satisfied: (1) that the random error for all the provenances or progenies tested is normally distributed; and (2) that the variances of provenances or progenies are homogeneous.

The random error of a single-tree plot test consists of two parts, namely, variation due to genetic make-up within each of the provenances or progenies tested; and variation due to uncontrolled environmental factors. Since most forest trees reproduce by cross pollination, the variation within a provenance or progeny is greater than that of self-pollinated crops. Even with a control-pollinated cross involving only two parents, all individual trees of the F_1 do not have the same genetic make-up because of the effects of segregation. Such genetic variation, especially in the case of controlled pollination, is not necessarily distributed normally in the offspring. Although the environmental variation can be safely assumed to be normally distributed, the total variation due to genetic and environmental factors may or may not deviate from normality depending on the type of genetic variation and the relative magnitude of genetic and environmental variation.

In cases where the genetic variation is

abnormally distributed and has a similar or greater magnitude than the environmental variation, data from a single-tree-plot test can not be validly analyzed with the ordinary methods. It is very difficult to estimate the genetic and environmental variations separately for most tree species since a large quantity of gentically homogeneous materials is impossible to obtain. However, the total random error due to genetic and environmental variation can be estimated from any provenance or progeny sample tested. The normality of distribution should then be checked before carrying out the analysis of variance. By using the "fixed model" of analysis of variance in a randomized block design, we have:

$$e_{ij} = X_{ij} - (X_{i.} + X_{.j} - X_{..}),$$

where,

e_{ij} = random error for j-th provenance in i-th block,

X_{ij} = the observation for j-th provenance in i-th block,

$i = 1,2,3,\ldots\ldots\ldots\ldots, r,$

$j = 1,2,3,\ldots\ldots\ldots\ldots, n,$

$\overline{X}_{i.} = \sum_{j=1}^{n} X_{ij}/n,$

$\overline{X}_{.j} = \sum_{i=1}^{r} X_{ij}/r,$ and

$\overline{X}_{..} = \sum_{i=1}^{r} \sum_{j=1}^{n} X_{ij}/rn.$

Test of normality as suggested by Pearson (1936) and Geary (1935) can be used to check the distribution of e's when the size of sample is large. The testing procedure is demonstrated in detail by Snedecor (1956). Box (1953) cited other workers' results and suggested that the comparative tests on means, such as "t" and "F," are remarkably insensitive to "general" non-normality of the parent population. By "general" parent non-normality is meant that the departure from normality, with respect to skewness, is the same in the different groups. However, if the skewness is in different directions in the different groups, such as may be expected in tree progeny tests, the results of ordinary statistical tests may be considerably affected.

The homogeneity of variance refers to the uniformity of variances within provenances or progenies tested. When the source of variance is predominantly from the environmental effects such as is the case in most agricultural crops, the assumption of homogeneity of variance may be valid, but provenance or progeny test samples of forest trees will frequently not satisfy this assumption, and single-tree plots are therefore not usable. Bartlett's test of the homogeneity of variances (Snedecor 1956) is required for checking data obtained from a completely randomized design. Graybill (1954) also suggested a method for testing the variance heterogeneity in a randomized block design. According to Box (1953), the Bartlett test is almost as sensitive for testing non-normality as for testing heterogeneity of variances.

The abnormality of random error in a single-tree-plot design was reported by Blake (1959) on red pine, a species with comparatively small genetic variation within any provenance. But since a high degree of genetic diversity appears to be characteristic of jack pine, provenance or progeny tests of this species with a single-tree-plot design probably will fail to satisfy both the "normality" and "homogeneity" requirements. Under these circumstances, Box (1953) suggested use of the Welch (1951) and James (1951) proposals by using the weighted within-groups variance as demonstrated by Snedecor (1956). The power of Welch's test is probably lower than the ordinary test of analysis of variance when the underlying assumptions are satisfied. How the gain of the single-tree-plot design in reducing variance compensates for the loss due to the failure to satisfy the underlying assumptions for the tests involved is difficult to say. In any event, a single-tree-plot design is not always as efficient as it may appear to be.

In a multiple-tree-plot design, the experimental unit is a group of trees. The

components of random error from unit to unit differ from those of a single-tree-plot test. Suppose that a single-tree-plot test gives a variance in error terms of, say, s^2 which consists of the genetic variations s_g^2 and the environmental effect s_e^2. Let the number of trees per plot in a multiple-tree-plot design be n, then a multiple-tree-plot design with r replications is physically equivalent to a single-tree-plot test with rn replications. Empirically, the standard error of the mean for the single-tree-plot test can be expressed as:

$$s_{\bar{x}} = \sqrt{\frac{s_g^2}{rn} + \frac{s_e^2}{rn}}$$

The standard error of the mean for the multiple-tree-plot test,

$$s'_{\bar{x}} = \sqrt{\frac{s_g^2}{rn} + \frac{s_e^2}{rn^g}}$$

where g, usually less than 1 (Sukhatme 1954), is a function of the variability of the testing site. It also is an important factor in determining the efficiency of a single-tree-plot design. When g equals 1, the testing site varies in a random pattern, hence, a multiple-tree-plot design is as efficient as a single-tree-plot test. The smaller the g value, the closer the relationship between adjacent plots, and the higher the efficiency of a single-tree-plot design. However, the most important function of the multiple-tree-plot design is to normalize the genetic variation and reduce the role played by genetic variation in the total random error. Tree species with abnormal and heterogeneous genetic variances will tend to be normally distributed and show a homogeneous random error under a multiple-tree-plot test.

Aside from the question of efficiency, another important consideration that must inevitably influence the decision to use single- or multiple-tree plots is the specific purpose of the provenance or progeny test. Although there are many types of provenance or progeny tests, the adaptation test is of most importance at the initial stage. For the adaptation test, interest centers on the resistance to climatic, disease and insect injuries exhibited by the material. Although provenances or progenies with a high degree of resistance to climatic and pest injury do not necessarily guarantee a successful final crop, trees sensitive to climatic extremes or susceptible to pest injuries at early stages are certainly less promising. A single-tree plot may be expected to yield valid data on resistance to many injuries and growth characteristics in the juvenile period since measurements at this stage are not confounded by competition and other deviations from stand conditions. The single-tree-plot design thus has great merit as a tool for weeding out progenies or provenances with poor juvenile characteristics.

After the juvenile period of development is passed and competition begins, the single-tree plot no longer resembles actual stand conditions found in nature or in plantations. Differences in growth rate and certain quality characteristics such as knot defects, taper and density, and even resistance to injuries may be observed between single-tree and multiple-tree-plot tests. Some conclusions derived from a single-tree-plot test may thus not be valid when transposed to actual outplanting conditions.

A striking example is provided by the jack pine budworm (*Choristoneura pini* Freeman) which selectively attacks the dominant and codominant trees in a stand. Such preference is apparently due to the fact that the young stage of the larvae feed on the male strobili which are typically more abundant on dominant and codominant trees. Suppose a single-tree-plot test of several jack pine seed sources is made. If it is assumed that Provenance *A* has a genetically better growth rate, the individuals of Provenance *A* will tend to assume dominant or codominant positions in the stand. This, in turn, will increase the probability of attack by the budworm, and Provenance *A* will suffer some growth reduction. Provenance *A* may thus show no

significant difference in growth rate from the other provenances. An interpretation that Provenance *A* does not grow better than others and is more subject to budworm attack is a fallacy.

The white pine weevil (*Pissodes strobi* Peck) also prefers dominant trees, hence, a single-tree-plot design for white pine is not desirable if this insect is present in areas where the tests are conducted.

Wright and Freeland (1959) recommended that when a single-tree-plot test is used, thinning should be done through the elimination of undesirable provenances as time goes on. This may result in the following complications: (1) the desirable provenances may not be distributed so ideally that evenly spaced individuals are obtained; and (2) individuals of a given provenance will be subjected to different degrees of competition, hence, an increase in the variance within provenance will reduce the efficiency of the test. In short, to test any characteristic influenced by stand conditions, the multiple-tree plot with a fairly large number of trees per plot is preferred.

Shape of Plot

In a multiple-tree-plot test, the shape of plot will also influence the efficiency of the test. Theoretically, a rectangular plot extended along the direction of the gradient gives the smallest variance. Hence, from the standpoint of efficiency, a long narrow plot with its longer side extended along the gradient line should be used. Such a decision, of course, depends on knowledge that a gradient does in fact exist. Given a plot size and number of treatments, Cochran (Federer 1955) has graphically presented the case for choosing the optimum plot shape in testing agronomic crops. He found that the rectangular plot gives, on the average, a smaller variance than the square plot. Therefore, he recommended the use of long narrow plots even when the gradient is not known.

Due to the special nature of forest tree tests, however, the foregoing recommendations need some reconsideration:

1. Unlike agricultural crops, the gradient of testing site for forest trees cannot be predetermined practically. Judging the variation of site from existing vegetation is also not reliable due to the difference in site requirements between present species and the trees tested and the unknown historical variation within the testing site.

2. The study of tree characteristics that may in any way be influenced by growing in stand conditions is the main function of multiple-tree-plot designs. Elimination of the border effect, necessary in order to duplicate stand conditions, can be done by either excluding the border rows of each plot when measured, or by planting an isolation strip of another progeny or seed source between plots. Exclusion of the border trees is to be preferred since a closer approximation of actual stand conditions for the material being tested is thus obtained. The number of trees excluded from measurement in a square plot is less than that in a rectangular plot. Hence a square plot will yield a higher percentage of usable data than a rectangular plot.

3. Cochran, in his illustration, computed the mean variance for a long narrow plot by averaging the most favorable and most unfavorable conditions and compared this with the most unfavorable result of the square plot design. Actually the square plot may also contain different levels of fertility, hence the average variance should be smaller than the figure given by Cochran. His conclusions that the overall mean variance for the long narrow plot is still smaller than that for the square plot is sound. However, the variance of the square plot tends to have a narrower range. In other words, the square plot has a consistent efficiency. Since forest tree tests are usually conducted over a long period of time on sites where fertility and other gradients are not known but where position effects caused by such gradients are, nevertheless, fixed and accumulative, we believe it is better to use a design with con-

sistent efficiency, such as a square plot, rather than a long narrow plot.

Some Recommendations

The following recommendations are made to make provenance or progeny tests of forest trees more reliable, sensitive and useful:

Replication by "years." Replications are necessary in any reliable test or experiment. The main functions of replication are: (1) to make possible the determination of the magnitude of the uncontrolled variation which is usually referred to as the error; (2) to give an effective control over experimental error; (3) to increase the precision of the test; and (4) to enlarge the scope of the experiment without increasing the experimental error.

Actually, the replication of an experiment is nothing more than stratification of the experiment into several parts such that the uncontrolled error is more homogeneous within each part. The best way to effect the replication is to select suitable criteria for stratification. The criteria selected should be factors which are not being tested intentionally but will affect the experimental error.

In a provenance test, "environmental diversity within location," "environmental diversity between locations" and "climatic fluctuation from year to year" are all important factors to be considered. Most provenance tests currently established are replicated by "within location" and "location" to control the positional variation. Very few studies have been replicated by "year." Conclusions obtained from a test without replication by "year" are valid only when control-pollinated progenies are tested and the climatic fluctuation from year to year in the testing area is negligible. In the case of open-pollinated provenances, or great yearly fluctuation in weather conditions at the test site, predictions of performance based on a single year's seed collection or a one-year test is rather risky. In areas where climatic fluctuations from year to year are negligible, replications by "year" may be accomplished by mixing several years' seed collections in a proportion similar to the seed production rate for each year.

Inclusion of a standard to select a group of genetically superior materials. As previously mentioned, mass production of selected provenances or progenies for commercial planting is rather slow. In such cases, it is better to select a group of genetically superior materials in order to obtain an ample source of supply for commerical uses. Besides, a mixture of provenances or progenies of different genetic constitution will give greater insurance against failure. As a means of selecting the superior seed sources or progenies, a standard or check should be included in the test. The local seeds or seeds commercially available and generally used by local nurseries can serve as the check. In the future analysis, an "*F*" test will be performed first by ordinary analysis of variance. A one-tailed *t*-test (Dixon & Massey 1957) may then be used to pick out provenances that are superior to the check. Provenances or progenies inferior to the check will be ignored and no further test is needed among them. In the superior group, Duncan's multiple range test (Federer 1955) may be used for further selection.

Use of a two-stage selection system. Perhaps the ideal system for provenance or progeny testing forest trees is to use single-tree plots and multiple-tree plots jointly. The single-tree plot would be used as the first stage in selection to weed out provenances which show poor performance in the juvenile period. The first stage might be carried on for a period of five to ten years depending on the growth rate of trees involved and the original spacing. In any case, the testing results would be evaluated when the competition among trees became evident. Since the single-tree plot is more efficient than the multiple-tree plot, the number of trees required for each provenance or progeny is small, say 30 to 50

plants. Under such conditions it would be feasible to include a large number of provenances in the test, hence, the chance of getting some desirable materials would be greatly increased.

The second stage test would employ a multiple-tree-plot design with a fairly large number of trees per plot, say 49 to 100. Only provenances showing a promising performance in the single-tree-plot test would be used. To test such characteristics as yield per unit area, thinning response, knot defects, taper, etc., under stand conditions, a complete commerical rotation will be required. Plots with a small number of trees are not recommended because: (1) such plots do not resemble stand conditions, and (2) the percentage data for mortality or incidence of injury obtained from such plots are difficult to analyze and interpret.

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Synthetic Culture of Mycorrhizae Of Southern Pines

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IDENTIFICATION of the fungal complement of mycorrhizae of forest trees is necessary before exhaustive studies on the relationship between the two symbionts can be made. Ideally, the fungus should be isolated directly from the mycorrhiza as collected in the field and identified. This, unfortunately, has seldom proved feasible, but new techniques are giving encouraging results. First, attempts to isolate the organism in pure culture either from soil or from the roots themselves have generally failed even though living fungal hyphae can be readily observed in fresh mycorrhizae. And, second, mycelium alone usually is not sufficient to identify the fungal partner. A sporophore is needed for positive determination, but fruiting has proved difficult to induce artificially with some fungi, and has not been obtained at all with most.

These obstacles were in large part circumvented by the development of the pure culture technique for mycorrhizal synthesis by Melin (1921). His method is now standard for ascertaining which fungi are capable of forming mycorrhizae when associated with roots of forest trees. A seedling is germinated aseptically and planted in a sterile nutrient medium to which inoculum of the suspected mycorrhiza-forming fungus is added. After 3 or 4 months roots are examined for the presence of mycorrhizae.

In the United States, Doak (1934b) employed this technique to determine the mycorrhiza-forming capacity of a number of fungi with several species of pine. He obtained typical ectotrophic mycorrhizae with the following combination of fungi and roots of pine seedlings: *Boletus bicolor* Peck with *Pinus rigida* Mill.; *B. brevipes* Peck with P. *rigida* and P. *taeda* L; B. *chromapes* Frost. with *P. taeda*; *Boletinus pictus* Peck with *P. strobus* L., *P. taeda*, P.*resinosa* Ait., and P. *rigida*; *Cantharellus cibarius* Fr. with *P. rigida*, *P. taeda*, and *P. strobus*; *Russula lepida* Fr. with P. *rigida*, P. *taeda*, and P. *strobus*; and *Scleroderma vulgare* (Horn.) Fr. with *P. strobus*.

Mycorrhizal formation by *Lepiota rhacodes* (Vitt.) Quél. with roots of *P. virginiana* Mill. was demonstrated similarly by Hacskaylo (1953). More recently Hacskaylo and Palmer (1955) reported the formation of ectotrophic mycorrhizae on *P. virginiana* by *Amanita caesaria* Schw., *A. frostiana* Peck, *A. rubescens* S. F. Gray, *B. bicolor* Peck, *B. variegatus* Fr., and *Rhizopogon roseolus* (Corda) Th. Fr.

The pure culture technique for mycorrhizal synthesis was employed in the present study to identify fungi entering into symbiotic relationship with roots of the four major southern pine species—shortleaf

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pine (*Pinus echinata* Mill.), loblolly pine (*P. taeda* L.), slash pine (*P. elliottii* Engelm. var. *elliottii*), and longleaf pine (*P. palustris* Mill.). This report represents part of a broad investigation of mycorrhizae of these species aimed at understanding their relationship to root pathogens and other organisms in the rhizosphere and to nutrition.

Materials and Methods

Only species of Hymenomycetes collected in the Piedmont and Coastal Plain regions of the Southeast were utilized in the present study. Both pine and pine-hardwood stands containing one or more of the test pine species, shortleaf, loblolly, slash, and longleaf pines, were canvassed. The most common genus encountered was *Boletus* followed by *Russula*, *Amanita*, and *Lactarius*. A species of *Clitocybe*, *C. laccata* (Scop.) Quél., has been collected in pine stands from western North Carolina to northern Florida, fresh sporophores being found throughout the year in the latter area.

Pure cultures of test fungi were obtained by removing small pieces of tissue from the context of sporophores and planting on malt extract and Hagem[1] agar media. Only about 5 percent of the isolations attempted are being successfully grown in pure culture. Some species showed improved growth when pine or hardwood-humus extract was added to the basic malt-extract medium. This was not correlated with their respective habitats. Addition of 25 ppm of thiamin to malt-extract agar appeared to aid growth of several species. Streptomycin incorporated in both malt extract and Hagem agar, at the rate of 80 ppm, was helpful in suppressing bacteria.

The following schedule was used to obtain sterile pine seedlings. Seed were first washed in detergent solution for 5 minutes, then rinsed in tap water. Next followed treatment in 1:500 mercuric chloride solution. Shortleaf pine seed were sterilized for 5 minutes; loblolly and slash pine seed for 12 minutes; and, longleaf pine seed were first hulled and then sterilized for 15 seconds. Thorough rinsing of seed in several changes of sterile water followed. The seed were then planted on cornmeal agar and placed in the refrigerator at 6° C for two weeks to break dormancy. After refrigeration, the planted seed were germinated at room temperature.

Sterile, germinating seedlings were removed from the agar and planted in 2-liter Erlenmeyer flasks containing vermiculite medium, as recommended by Hacskaylo (1953), to which nutrient solution formulated by Melin (1921) and modified by Norkrans (1949) had been added. At the same time, or shortly thereafter, a bit of inoculum from a pure culture of the test fungus was planted in the vermiculite about 1 inch from the seedling. The flasks were held in the laboratory under artificial light for 10 days to confirm the absence of contamination, after which they were placed in a greenhouse fitted with 30 percent overhead slat shading. The bases of the flasks were immersed in a water bath maintained at 17° C to prevent excessive heating of the medium and the interior of the flask. On the hottest summer days the temperature of the vermiculite did not exceed 24° C.

After 3 to 4 months, the flask was opened, and a bit of vermiculite medium placed on nutrient agar to reisolate the fungus and to verify the purity of the culture. The seedling, now 5 to 7 inches tall and bearing secondary needles, was removed and the roots carefully examined for the presence and degree of development of mycorrhizae. Mycorrhizal root tips were severed and placed in weak chrom-acetic killing solution in preparation for later sectioning and microscopic examination to confirm the presence or absence of hyphal penetration.

Material for sectioning was dehydrated using Johansen's (1935) tertiary butyl al-

[1]Formula obtained by personal communication in 1959 from E. Hacskaylo, Plant physiologist, Forest Service, U.S. Department of Agriculture, Beltsville, Maryland.

cohol method. Sections were cut 12 microns thick. Satisfactory differential staining was obtained using ordinary safranin fast-green combinations, the orseillin BB and crystal violet schedule of Doak (1934a), and the safranin-picro-aniline blue method described by Jackson (1947).

Results and Discussion

The fungi thus far tested and results obtained with shortleaf, loblolly, slash, and longleaf pines are shown in Table 1. Synthesis of bifurcate, ectotrophic mycorrhizae with good mantle and Hartig net development on roots of all four pine species was demonstrated for *Clitocybe laccata*. Figure 1 illustrates typical hyphal mantle and Hartig net development on mycorrhizae of slash pine produced by *C. laccata* in flask culture. In all positive syntheses observed, the Hartig net hyphae developed between all cortical cells. Positive synthesis was also

TABLE 1. Results of synthetic culture of pine mycorrhizae.

Fungus	Pine species[1]				Description of mycorrhizae		
	Shortleaf	Loblolly	Slash	Longleaf	Form and type	Mantle development	Hartig net development
Amanita muscaria (L.-Pers.) Quél.	I	+	I	I	Bifurcate, ectotrophic	Good	Good
Boletus betula Schw.	—	—	+	—	Coralloid, bifurcate, ectotrophic	Good	Good
B. communis Bull.	I	+	+	—	Bifurcate, ectotrophic	Good	Good
B. rubropunctus Peck	—	—	—	I			
B. spp. (Florida)	I	+	+	+	Coralloid, bifurcate, ectotrophic	Good	Good
Clitocybe laccata (Scop.) Quél.	+	+	+	+	Bifurcate, ectotrophic	Good	Good
C. piceina Peck	+	I	I	I	Bifurcate, ectotrophic	Fair	Fair
C. tabescens (Scop.) Bres.	—	—	—	—			
Cortinarius albidipes Peck	I	—	—	I			
Hypholoma spp.	—	—	I	I			
Lactarius spp. (Florida)	+	—	—	—	Bifurcate, ectotrophic	Good	Good
Lycoperdon spp.	I	—	—	—			
Pisolithus tinctorius (Mich. ex Pers.) Coker and Couch	+	—	—	I	Coralloid, bifurcate, ectotrophic	Good	Good
Psalliota campestris (L.) Quél.	I	—	—	I			

[1] I, test incomplete; +, mycorrhizae formed; —, mycorrhizae not formed.

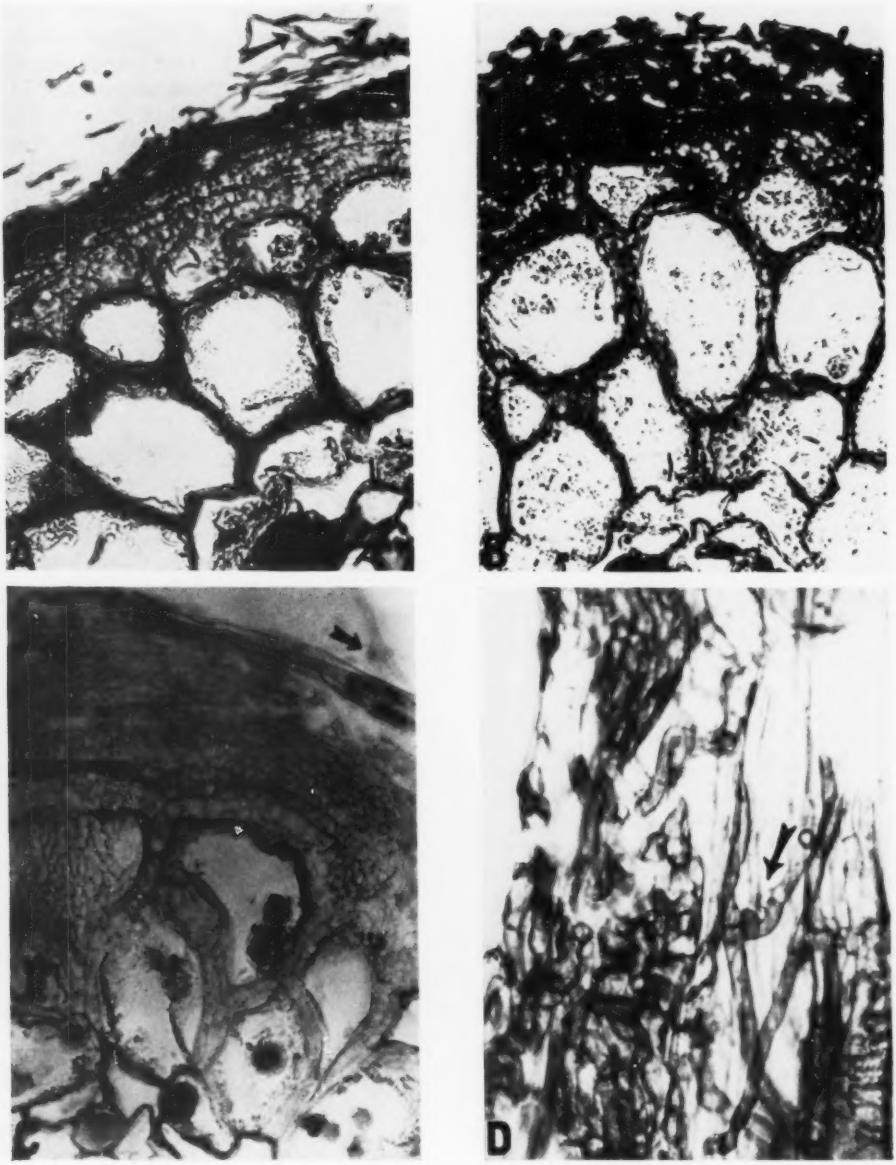

FIGURE 1. *Photomicrographs of sections of mycorrhizae produced on slash pine with* Clitocybe laccata. *Transverse sections in A* (× 3075), *B* (× 3225), *and C* (× 3375) *show well-developed fungus mantle and intercellular Hartig net. D, Longitudinal section of mantle* (× 4725). *Arrows point to clamp connections in mantle hyphae.*

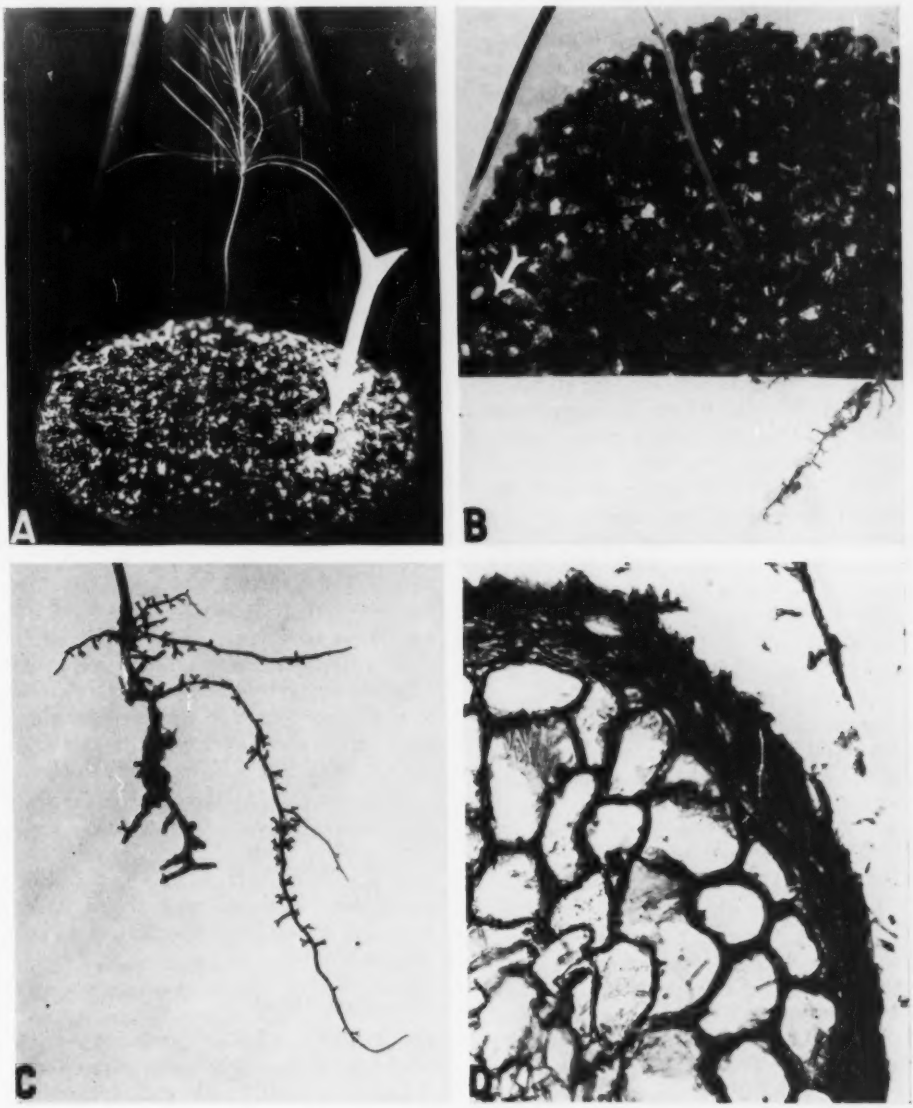

FIGURE 2. *Cultural and histological confirmation of mycorrhizal synthesis by* Boletus communis *on slash pine. A, Seedling growing in test flask—arrow points to sporophore of* B. communis *produced in the flask 52 days after inoculation. B, Test flask broken open to allow closeup view of sporophore (left, at arrow), connected by rhizomorphs to mycorrhizal root at right. C, Complete root system of test seedling, showing mycorrhizae and heavy mycelial envelopment. D, Transverse section of mycorrhiza from test seedling, with fungus mantle and intercellular Hartig net development (× 2870).*

achieved with the following: *Amanita muscaria* with loblolly pine; *Boletus betula* with slash pine; *B. communis* with loblolly and slash pine; *B.* spp. (unidentified, from northern Florida) with loblolly, slash, and longleaf pine; *Pisolithus tinctorius* with shortleaf pine; and *Lactarius* spp. (unidentified, from northern Florida) with shortleaf pine.

The widespread occurrence of *Clitocybe laccata* and the results of these tests indicate that this symbiont probably is an important mycorrhiza-former in pine stands of the Southeast. Sporophores have been found particularly abundant and widespread in slash and longleaf pine stands of northern Florida, where fresh specimens were collected throughout winter when other Hymenomycetes were lacking.

Woodruff (1933) earlier reported that *Boletus communis* was associated with mycorrhizal roots of pecan (*Carya illinoensis* (Wangenh.) K. Koch). Cultures of this Hymenomycete used in the present study were grown from sporophores collected beneath yard pecans in Athens, Georgia, where they grow in abundance from April to November during moist weather or when the lawn is frequently watered. Sporophores of *B. communis* have been collected only infrequently by the authors in forest stands of the Southeast. It is probable that this fungus is not important as a mycorrhiza-former in the pine stands of this region.

In the course of this work, two fungi, *Collybia radicata* (Fr.) Quél. and *Boletus communis*, produced sporophores in culture. Several test tube cultures of *C. radicata* growing at 25° C in the absence of light on Hagem's medium fruited after 6 to 8 months. The caps were about 1 cm in diameter, well formed, and discharged viable spores. The stipes were from 7 to 10 cm in length.

Fructification of *Boletus communis* occurred while in association with the roots of a 2-month-old slash pine seedling growing on vermiculite wetted with Melin-Norkrans' solution in a 2-liter flask. Two small, well-developed sporophores, one 1.0 cm and the other 1.5 cm tall, rose from the surface of the medium (Fig. 2A). The flask was later broken open and rhizomorphs extending from the fruiting bodies traced directly to mycorrhizal roots of the seedling (Fig. 2B).

Summary

The pure culture technique for mycorrhizal synthesis was employed to identify fungi producing mycorrhizae in association with roots of shortleaf, loblolly, slash, and longleaf pine. Fourteen species of Hymenomycetes were tested with one or all four species of pine. Mycorrhizal synthesis has been demonstrated for eight of these.

Clitocybe laccata was found to produce mycorrhizae with roots of all four pines: shortleaf, loblolly, slash, and longleaf. These results and the widespread occurrence of *C. laccata* in the Southeast suggest that this fungus is an important mycorrhiza-former in the pine stands of this region.

The fungus, *Boletus communis*, commonly associated with mycorrhizal formation with pecan was found also to produce well developed ectotrophic mycorrhizae with roots of both loblolly and slash pine.

Two cases of fruiting by test fungi in culture are reported. One, *Collybia radicata*, produced well-formed fructifications on Hagem's medium. The other, *Boletus communis*, developed sporophores when grown in association with roots of a slash pine seedling.

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Forest and Shade Tree Entomology

By Roger F. Anderson, 428 pp. Illus. John Wiley and Sons, New York and London, 1960. $8.50.

Review by V. M. Carolin, Jr.
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One of the pressing needs in forest entomology is for a comprehensive text that provides a background in basic entomology, discusses principal forest insect pests in both eastern and western North America, and relates this information to economic problems in survey and control. The author has seen this need and approached it boldly. Section I of the text deals with two of the needs—basic entomology, and survey and control aspects. Section II is concerned with a large number of forest and shade tree insect pests, for which identification aids and biological information are provided. The listing of selected references shows that the author has tapped the recent literature.

In Section I the fundamentals of entomology are covered adequately in 48 pages. The subsequent discussion on insect control is adequate, except that some statements on natural control appear to be based on opinion, rather than fact. Chapters on insecticides and methods of application are astutely written. The chapter on forest insect surveys, however, has several shortcomings. For example, the generally accepted guidelines formulated by Bongberg for defining types of surveys and their aims have not been consulted. The terminology used by the author is therefore not meaningful, and the concept of biological evaluation is totally omitted. In addition some misleading statements are made in regard to the type of personnel who should perform aerial surveys, the factors involved in timing intensive surveys, and the distinction between relative and absolute populations.

Section II is the real meat of the text, and the keys to insect species are likely to be very useful. Type of tree damage is used to separate broad insect groups, as in U. S. Dept. Agric. Miscellaneous Publication 273 (Insect Enemies of Western Forests). Thereafter, insect characteristics and habitat are used for recognition, with increasing emphasis on structural details of the insect. This is as it should be; field identification will never be reliable unless foresters are willing to look more closely at the insect. For each major species information is given on injury, hosts, range, insect appearance, life cycle, and control. Numerous photographs of good quality accompany this part of the text. Where a species occurs both in the East and West, the detailed information given is usually for eastern conditions. In some cases, this may be attributed to lack of formal publication by western workers.

The text is basically useful and attractively presented, although numerous printing and spelling errors are apt to annoy the reader. This is the type of text which can and should be revised in ten years and become increasingly useful to the forester and forest entomologist.

Utilization of Radioactive Ornithine by Germinating Embryos of Longleaf and Slash Pines

BY
ROBERT L. BARNES
AUBREY W. NAYLOR

A GROWING BODY of evidence is available that indicates seed plants can utilize the carbon chain of ornithine in the formation of several compounds (Naylor 1959). Decarboxylation of ornithine-2-C^{14} to the diamine putrescine has been shown to occur readily in potassium deficient barley and clover (Coleman 1957, Coleman and Hegarty 1957). Watermelon seedlings (Kasting and Delwiche 1957, 1958), mineral deficient clover and barley (Coleman and Hegarty 1957, Coleman 1958), and mung bean mitochondria (Bone 1959) are known to convert ornithine-2-C^{14} to citrulline. In the same plant material, excepting mung bean mitochondria, it was further noted there was active transfer of label from ornithine to glutamic acid and proline. These results parallel in several respects those reported for *Escherichia coli* (Vogel 1956).

Studies in this laboratory with isolated roots and callus tissue of pond pine (*Pinus serotina* Michx.) and sand pine (*Pinus clausa* (Chapm.) Vasey) (Barnes and Naylor 1959a) have provided evidence that these tissues utilize the carbon chain of ornithine-2-C^{14} in the formation of citrulline, arginine, glutamic acid and proline. It has further been shown that ornithine can serve as the sole source of nitrogen in the continuous culture of isolated roots of pond pine (Barnes and Naylor 1959b). In such cultures arginine or citrulline can be substituted for by ornithine. The importance of ornithine as a metabolic intermediate in pine tissue was thus indicated. The present paper reports on the utilization of ornithine-2-C^{14} by embryos of longleaf pine (*Pinus palustris* Mill.) and slash pine (*Pinus elliottii* Englm.).

Materials and Methods

Seeds of longleaf and slash pines were surface sterilized in dilute sodium hypochlorite solution (made from commercial Clorox), rinsed with sterile water, and placed on 1.0 percent agar in Petri dishes. The procedure followed was essentially the same as that used in obtaining pine roots for *in vitro* culture (Barnes and Naylor 1959c). At intervals of 0 to 15 days, samples of seed—5 longleaf and 10 slash pine—were selected for uniformity.

The seed coat and endosperm were then removed aseptically leaving a freed embryo. Each of the germinating embryos was placed in an incubation medium consisting of 2 microcuries of DL-orithine-2-C^{14} (Tracerlab, Inc.), and 100 microliters of 0.01 M phosphate buffer, pH 6.6, contained in a 2.0 ml Pyrex volumetric flask.

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Another useful vessel for this purpose was the cut off conical end of a 2.0 ml centrifuge tube. A film of liquid always covered the root. With but one exception, all embryos were incubated in darkness. The 15-day longleaf pine seedlings, which had well developed roots, cotyledons and primary needles, were incubated in light. Similar-aged slash pine embryos had developed only a short primary root.

After a 24-hour incubation period with DL-ornithine-2-C^{14}, the embryos were prepared for analysis. They were washed free of adhering test solution with water, then placed in 12 ml graduated centrifuge tubes containing enough boiling 80 percent ethyl alcohol to cover the embryos. Boiling was allowed to occur for one minute whereupon the extract was decanted into another 12 ml centrifuge tube. Two further one-minute extractions were made with boiling water. Previous experience with such tissues had shown that this procedure results in essentially complete removal of alcohol and water soluble radioactive compounds; furthermore, there is very little transformation of glutamine to pyrrolidone carboxylic acid.

The 15-day longleaf pine seedlings were separated into roots, cotyledons, and tops (hypocotyl, epicotyl and primary leaves) before being extracted. The combined ethanol-water extracts were then reduced, at room temperature, to 0.1 ml by blowing a stream of dry filtered air over the surface. An aliquot of the straw colored concentrate was then spotted on sheets of 18¼" x 22½" Whatman No. 1 filter paper for two dimensional chromatography. Before development, the radioactivity in the spot on the origin was determined and recorded.

Chromatography was then carried out with water saturated phenol in the first direction and n-butanol-propionic acid-water in the other (Benson *et al.* 1950). Following development, the chromatograms were placed in contact with 14 x 17 inch Eastman No-Screen Medical X-ray film and left for two to three weeks to locate the substances on the paper possessing most of the radioactivity (Benson *et al.* 1950). The amount of radioactivity contained in each compound was determined by counting the area directly on the paper with a large Geiger-Müller tube (Fuller 1956).

Tentative identification of the compounds containing radioactivity were made by comparison of R_f values with known compounds chromatographed under similar conditions. Further identification was by means of co-chromatography and specific spray reagents prepared and used in accordance with procedures compiled by Block *et al.* (1958). Carbohydrates were detected with p-anisidine-HCl and amino acids with a ninhydrin spray that gives distinctive color reactions with different amino acids (0.1 gm ninhydrin, 5.0 ml lutidine, 5.0 ml collidine, 90 ml 95 percent ethanol). Citrulline was further tested for with Ehrlich's reagent and arginine by means of the Sakaguchi reaction.

Data on radioactivity in the several compounds deriving label from DL-ornithine-2-C^{14} have been calculated in terms of the percentage distribution of C^{14} metabolized from DL-ornithine-2-C^{14}. What is shown, therefore, is the percentage of the derived label present in any one compound in the different aged embryos.

Results

The results of supplying radioactive ornithine to longleaf pine embryos at several stages of germination are given in Table 1. In the youngest embryos used citrulline, arginine, glutamic acid and proline, in that order, were found to have the highest percentages of label derived from DL-ornithine-2-C^{14}. As germination progressed, the trend seemed to be toward lower percentages of derived label in citrulline and proline and higher percentages in arginine after 24 hours exposure to ornithine-2-C^{14}.

In 15-day-old longleaf pine seedlings the percentage of derived label in citrulline was quite small. Roots and tops accumulated higher percentages of label in arginine and asparagine than did the cotyle-

TABLE 1. Relative radioactivity of compounds formed during metabolism of DL-ornithine-2-C^{14} by germinating embryos of longleaf pine.[1]

Compound	Time of germination (days)							
						15		
	0	1	2	6	10	Roots	Cotyledons	Tops
Aspartic acid	Tr	1	1	1	1	3	----	2
Glutamic acid	18	12	20	16	18	15	17	14
Serine[2]	----	----	----	----	----	5	19	4
Sucrose	----	----	----	----	----	8	31	10
Asparagine	----	----	----	----	Tr	4	----	7
Glutamine[3]	+	+	+	+	+	9	6	+
Arginine	26	28	24	36	50	39	8	48
Citrulline[3]	38	40	36	27	18	+	7	+
Alanine	1	1	1	1	1	1	Tr	2
Proline	8	10	8	5	4	3	5	2
γ-aminobutyric acid	2	4	2	5	2	5	6	2
Citric acid	2	1	2	2	2	3	Tr	2
Malic acid	3	2	5	5	2	3	Tr	4
Unknowns	2	1	1	2	2	2	1	3

[1]Figures represent percentages of total activity on autoradiograms, exclusive of that in ornithine.
[2]Figures for serine may include small amounts of glucose.
[3](+) signs indicate compounds were present in small amounts, but were masked by arginine.
Tr = trace amounts (less than 1%).

TABLE 2. Relative radioactivity of compounds formed during metabolism of DL-ornithine-2-C^{14} by germinating embryos of slash pine.[1]

Compond	Time of germination (days)					
	0	1	2	6	10	15
Aspartic acid	Tr	Tr	2	3	2	1
Glutamic acid	20	50	48	52	51	38
Glutamine	39	10	16	6	7	25
Arginine	----	----	----	4	9	
Citrulline	19	14	11	10	14	20
Alanine	----	Tr	----	1	1	2
Proline	8	13	10	9	9	3
Citric acid	4	5	4	6	2	3
Malic acid	11	8	9	8	6	6
Unknowns	----	----	----	1	----	2

[1]Figures represent percentages of total activity on autoradiograms, exclusive of that in ornithine.
Tr = trace amounts (less than 1%).

dons. On the other hand, the cotyledons were richest in labeled serine, citrulline, and sucrose. Some of the label in sucrose probably was derived from $C^{14}O_2$ produced through degradation of ornithine-2-C^{14} and subsequent fixation in phosphoglyceric acid by photosynthetic reactions followed by sugar and serine synthesis. It should be particularly noted that all organs of the 15-day-old seedling transferred

approximately equal percentages of C^{14} from the metabolized ornithine into glutamic acid and proline.

Slash pine embryos showed percentages of label in all of the compounds deriving label from DL-ornithine-2-C^{14} that were quite different from those found in longleaf pine at the several stages of germination (Table 2). When comparing Tables 1 and 2, it will be noted that at each stage of germination slash pine embryos tended to have higher percentages of activity in glutamic acid than in arginine or citrulline after 24 hours in the presence of DL-ornithine-2-C^{14}. The percentage of label transferred to glutamine was greater in slash pine embryos than in longleaf pine. Observe, also, that the percentage of activity in the citric acid cycle compounds was higher in slash pine than longleaf pine embryos. Label from DL-ornithine-2-C^{14} was not detected in the arginine of slash pine embryos until the six day embryos were used. With increase in age after that, there was an increase in percentage of label in arginine at the end of the incubation period.

Discussion

There appeared to be changes in the rate of arginine synthesis in longleaf pine embryos as germination progressed. Since quantitative data on pool sizes are not available, however, one can not be certain about how great the changes were. Yet on a qualitative basis it was clear that the longleaf pine embryos accumulated arginine to an increasing degree as germination proceeded.

As this was occurring, a trend developed in which smaller percentages of label from ornithine accumulated in citrulline and higher percentages of activity were found in arginine. Large increases in free arginine may have metabolic consequences of a growth regulating nature. Antagonism between arginine and lysine has been noted in a *Neurospora crassa* mutant, a 50 percent inhibition in growth occurring when there was an arginine-lysine ratio of one (Doermann 1944). In *Escherichia coli* ornithine transcarbamylase synthesis was demonstrated to be inhibited within a few minutes after the arginine content of the medium was increased (Maas 1958). It is too early to say, however, if free arginine has a growth regulatory effect in longleaf pine.

Since arginine is a constituent of plant proteins, often accounting for 20 percent or more of the amino acid residues, the importance of a smooth functioning ornithine → citrulline → arginine pathway in amino acid metabolism is apparent. Hydrolysates of protein from the embryos exposed to DL-ornithine-2-C^{14} for 24 hours showed that radioactive arginine was being produced and incorporated into proteins formed during the incubation period.

Glutamic acid and proline are also constituents of proteins, and the general significance of glutamic acid in metabolism is well recognized. The fact that proline and glutamic acid became well labeled from radioactive ornithine supports previous indications of close interrelationships of these three amino acids in the metabolism of pine tissues (Barnes and Naylor 1959a). Radioactive proline and glutamic acid were both found in protein hydrolysates following incubation of the embryos with DL-ornithine-2-C^{14}.

The cotyledons of the 15-day-old longleaf pine seedlings appeared to be functioning actively in photosynthesis, as was indicated by the large amounts of radioactive sucrose and serine, typical major products accompanying photosynthesis (Norris *et al.* 1955). The source of the radioactive CO_2 used in photosynthesis is not known. Ornithine labeled in the C_2 position would not be a direct supplier. Presumably, the $C^{14}O_2$ arose from decarboxylation of one of the citric acid cycle acids after sufficient distribution of label from ornithine had taken place.

Cotyledons of 15-day-old longleaf pine seedlings had higher percentages of label in citrulline and less in arginine than other portions of the seedling after comparable incubation periods (Table 1). The roots

appeared to be an active site of amide synthesis, judging from the percentage of label they accumulated. Bollard (1957) has shown that asparagine and glutamine are among the major constituents of the organic nitrogen fraction of xylem sap in many woody species, including pine. Roots of several herbaceous species synthesize amides readily (Naylor *et al.* 1958). Very likely, there is considerable export of amides from roots to the tops of intact plants.

Although citrulline became labeled in the slash pine embryos during the initial inhibition period, when DL-ornithine-2-C^{14} was present, no radioactivity appeared in the free arginine. This could be construed to indicate that arginine was not being synthesized. If, however, arginine was being used as rapidly as it was being synthesized during the early stages of germination and if "active pools" as well as "passive pools" exist in the cell, as has been indicated by Steward *et al.* (1958) and Folkes (1959), and the "active pool" was kept at minimum size during early stages of germination, then one can account for failure of arginine to show label in the alcohol-water extract. After being set to germinate for six days, the slash pine embryos began to have the ability to accumulate label in free arginine. From the sixth day on then, arginine synthesis in these embryos was in excess of the amount being used.

These experiments show clearly that when DL-ornithine-2-C^{14} is administered to embryos of longleaf and slash pine C^{14} appears in citrulline and arginine. It is, therefore, tempting to speculate that the classical Krebs-Henseleit (1932) ornithine urea cycle is operative in the embryos. Urea, however, was not found on our chromatograms and a cyclic process has not been demonstrated. The fact that proline and glutamic acid became labeled indicates that a pathway from ornithine to these two amino acids is operative. If the pathway is the same as in other organisms, a common intermediate should be glutamic semialdehyde.

Summary

1. *Pinus palustris* Mill (longleaf pine) and *Pinus elliotii* Englm. (slash pine) seeds were germinated for 0 to 15 days, and the embryos incubated in phosphate buffer at pH 6.6 with DL-ornithine-2-C^{14} for 24 hours.

2. By using two dimensional chromatographic techniques followed by autoradiography of the papers, it was possible to show trends in the use of the ornithine carbon skeleton by the embryos of the two species.

3. Longleaf pine embryos of all ages incubated with labeled ornithine tended to have about 18 percent of the derived label in glutamic acid at the end of the test period. The percentage of label in citric and malic acid was small—about 7 percent—but was approximately the same in all samples.

4. While two-thirds of the label from ornithine was in arginine and citrulline at the end of the presentation period for each germination stage of longleaf pine tested, the relative amounts of label in arginine and citrulline did change. At the end of the first 24 hours of germination, arginine had 26 percent of the C^{14} and citrulline 38 percent of the label derived from ornithine that was detectable on the chromatograms. But in the 6-day-old embryos the percentage of derived label in these two amino acids after a 24 hour incubation period was almost exactly reversed. In still older embryos arginine tended to accumulate even higher percentages of the derived label.

5. In all except the 0- and 15-day slash pine embryos approximately 50 percent of the carbon derived from the added ornithine was in glutamic acid when the 24 hour samples were taken. Up to 20 percent of the C^{14} was in citrulline in the same samples and 15 percent in malic and citric acid.

6. Protein hydrolysates made at the end of the 24 hour incubation periods with DL-ornithine-2-C^{14} contained radioactive arginine, proline and glutamic acid.

7. Neither non-radioactive nor radioactive urea was detected on the chromatograms. Thus a complete ornithine-urea cycle has not been established for longleaf and slash pine embryos.

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Detecting Defects in Wood by the Attenuation of Gamma Rays

BY
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How to detect and evaluate internal defects in trees and logs is a problem that has always plagued foresters. Until recent years the chief non-destructive means for testing living trees for hidden decay were visual inspection and sounding the tree with an ax or hatchet. All foresters are aware that neither of these methods results in anything more than an informed guess. A better method is sorely needed.

Recent advances in nuclear physics have suggested several new approaches to the problem. One of these involves the use of radioisotopes to "x-ray" wood and reveal its internal physical state.

The first non-destructive testing of living trees by means of x-rays and film was described by Maloy and Wilsey (1930). They devised a lead grid system to eliminate scattered radiations and obtained fair results but it was next to impossible to transport the equipment in the field. Zucker (1940) used motorized transportation and a somewhat similar apparatus to x-ray utility poles along highways. (The value of testing poles by means of x-rays was shown by Truman (1952) when he found 20 out of 33 utility poles which had been condemned by visual inspection, still to be usable.) Madson (1956) and McNabb (1956) partially solved the problem of mobility by developing a new lightweight (13 lbs.) x-ray unit with thulium as the source of x-rays and film as the detector. The New South Wales Forestry Commission of Australia (1955) and Iisuka of Japan (1956) have used radioisotopes in an effort to detect defects in wood when electronic type detectors were used.

New and more precise methods for detecting defects in wood have been developed during the past year by the Department of Zoology and Entomology at The Ohio State University in cooperation with the Central States Forest Experiment Station. The purpose of the study was to explore the possibilities of detecting defects in wood by means of the attenuation of gamma rays. The principle involved is simply that gamma rays passing through a solid object diminish as the thickness of the object increases. Such a method could be used for various purposes throughout the wood industry. If successful, it was known that a portable detector could be constructed.

Specifically, answers were sought to the following questions: (1) Can defects in wood be detected by means of the attenuation of gamma rays? (2) If so, can the extent of the defect be determined in this

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This paper is condensed from a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree at Ohio State University.

The author is now with the Miami Valley Hospital, Dayton, Ohio. He wishes to express his appreciation to his adviser, Willard C. Myser, Assistant Professor in the Department of Zoology and Entomology, and others who helped in various ways: M. L. Pool, Professor, Department of Physics; R. P. Sullivan and W. E. Carey, Research Assistants, Department of Physics; and O. Keith Hutchison, Forester, Central States Forest Experiment Station. This work was made possible by cooperative-aid funds provided by the Central States Forest Experiment Station and the U.S. Forest Products Laboratory. Manuscript received Jan. 7, 1959.

way? (3) What radiation energies would be most suitable for the job? (4) What type of detector would be the most suitable? and (5) What effect does moisture content of the wood have upon gamma attenuation?

Basic Mathematical Assumption

In order to consider the answers to several of these questions more thoroughly a mathematical description of the attenuation of gamma rays seems appropriate.

When a parallel beam of monoergic x-rays or gamma rays passes through any material, the intensity of the emergent beam is less than that of the incident beam. If the rate of the emergent beam is subtracted from the rate of the incident beam, the rate of absorption by the material is obtained. Therefore, the measurement of radiations, as described in this study, is that of the emergent beam and is the reciprocal of the rate of absorption by the absorber.

The decrease in intensity of the beam when it traverses a small thickness (dx) of the material depends upon the degree of absorption per unit of thickness. The basic mathematical assumption is

$$\frac{-dI}{I_o} = \mu_l dx$$

where I_o is the intensity of the radiations before passing through the absorber and $-dI$ represents the decrease in intensity after passing through an absorber of increasing thickness dx. The linear absorption coefficient μ_l is a symbol representing the fraction of energy removed from a gamma ray beam per centimeter of path of the absorber.

Which results in

$$I = I_o e^{-\mu_l x}$$

The values of I_o, e, and μ_l are constants; therefore, I and x are the only variables. Since x is an exponent, I will vary exponentially with a linear change in x. If the values of I are plotted on the logarithmic ordinate, of semi-logarithmic paper, and x on the linear ordinate, a straight-line curve will be formed. This means that the ratio of the kinds of atoms composing an absorber is consistent throughout its thickness.

Methods and Materials

Equipment and materials used in the study were: six different radiation sources, four species of wood, and three radiation detectors. The radiation sources were *Sn* 113, *I* 129, *Yb* 169, *Ce* 144, *Sm* 144 plus *n*, and *Cs* 137. The radiations from these sources ranged in energy from 23 to 661 Kev.

Wood species used were selected for their wide range in specific gravity: they were (1) sugar pine (*Pinus lambertiana* Dougl.), with a specific gravity of about 0.36 at 12 percent moisture content; (2) yellow-poplar (*Liriodendron tulipifera* L.), specific gravity between 0.40 and 0.50; (3) and hickory (*Carya* sp.) and black oak (*Quercus velutina* Lam.), which range in specific gravity from 0.64 to 0.74.

The detectors used were a scintillation spectrometer, a G-M counter circuit, and film.

Scintillation spectrometer. The scintillation spectrometer is a radiation detector that registers gamma rays of only one energy even though more than one gamma ray energy is incident upon its crystal. For example, three gamma ray energies of say, 100 Kev, 200 Kev, and 300 Kev may be incident upon the crystal but, by proper adjustment of the scintillation spectrometer only the 200 Kev gamma rays may be measured. This type of radiation detector may be more than 10 times as sensitive to gamma rays as a G-M counting circuit.

Geiger-Müller tube. The Geiger-Müller tube, of the G-M counting circuit, is a gas-filled, two-electrode, ionization chamber. A gamma ray energy may be detected by a G-M counting circuit if it is absorbed in the wall of the G-M tube and ejects an electron or a positron into the sensitive volume of the tube. As used in these experiments, and in contrast to the scintillation spectrometer, the G-M counting circuit was sensitive to all gamma ray energies which were incident upon the G-M tube. For example, three gamma

ray energies of say, 100 Kev, 200 Kev, and 300 Kev may be incident upon the G-M tube, but in this case all three energies would be measured.

Film. X-ray film was used as the detector of radiations because of its high sensitivity to x-rays and gamma rays. In some cases both front and back fluorescent screens were used with the film in order to increase its sensitivity to the radiations.

Procedures

Testing for uniformity in wood structure. The first step was to find out if solid wood is uniform enough in atomic structure to permit its density to be measured by the attenuation of gamma rays. To do this, a radioactive source was placed 14 inches below the sensitive crystal of a spectrometer and 24 12x12x½-inch sugar pine boards were piled, one at a time, in the space between. As each board was inserted, the intensity of the penetrating radiations was read on the spectrometer. These data were plotted on semi-log paper and the resulting straight line absorption curve indicates that the ratio of the kinds of atoms composing the structure of the pine absorber was consistent throughout its thickness (Fig. 1). (Apparently physical differences between spring and summer wood do not affect the ratio of kind of atoms.)

This test was repeated with yellow-poplar and black oak boards and two different radiation sources having different energies (*Cs* 137 with 661 Kev, and *Sm* 144 plus *n* with 38 Kev). Similar straight line curves resulted. Thus, wood from 3 species of trees each having a different density shows consistency of structure. It is reasonable to believe that other species of wood would show similar consistency. Therefore, if an inconsistency in wood is noted by means of attenuation of gamma rays, it may be considered as a defect in the wood.

The choice of a suitable radiation source depends upon the density of the absorber, the kinds of atoms it is composed of, and resolution desired. As these studies progressed the range of energies deemed best suited to the purpose was narrowed down to a low of 23 Kev for the less dense species and a high of 135 Kev for the more dense species.

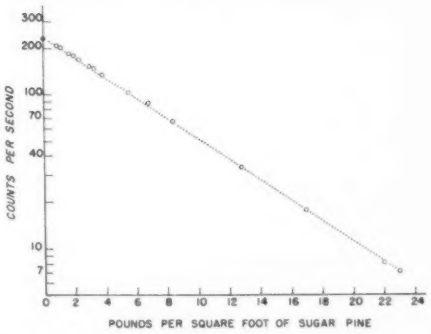

FIGURE 1. *Absorption curve for sugar pine made with scintillation spectrometer using Sn 113 x-ray of 23 Kev.*

Most of these experiments were repeated using a G-M counter. Regardless of the source or the density of the wood, absorption curves made with a G-M counter circuit show a decrease in slope with an increase in the thickness of the respective absorber. This is because the G-M counter as used recorded all the radiations that struck the tube instead of only a specifically selected radiation energy as is possible with the scintillation spectrometer.

Detecting gaps in solid wood. The next step was to see if gaps or spaces in solid wood could be detected using the same equipment and methods. One, two, and three of the ½-inch boards were removed from inside the 12-inch-high pile of sugar pine and spacers inserted to leave ½-, 1-, and 1½-inch spaces in the pile. The location of these spaces was varied in the pile, and the remaining pile was measured (Fig. 2).

Even a ½-inch space or defect could be easily detected and its location in the pile had little to do with its resolution. The 1½-inch space caused by the removal of three boards shows approximately a 35-percent difference from that point at which

no boards were removed. The 1-inch space showed approximately a 24-percent difference and the ½-inch space showed approximately an 11-percent difference from that point at which no boards were removed.

Detecting holes in logs. Logs were passed in a direction parallel to their diameters

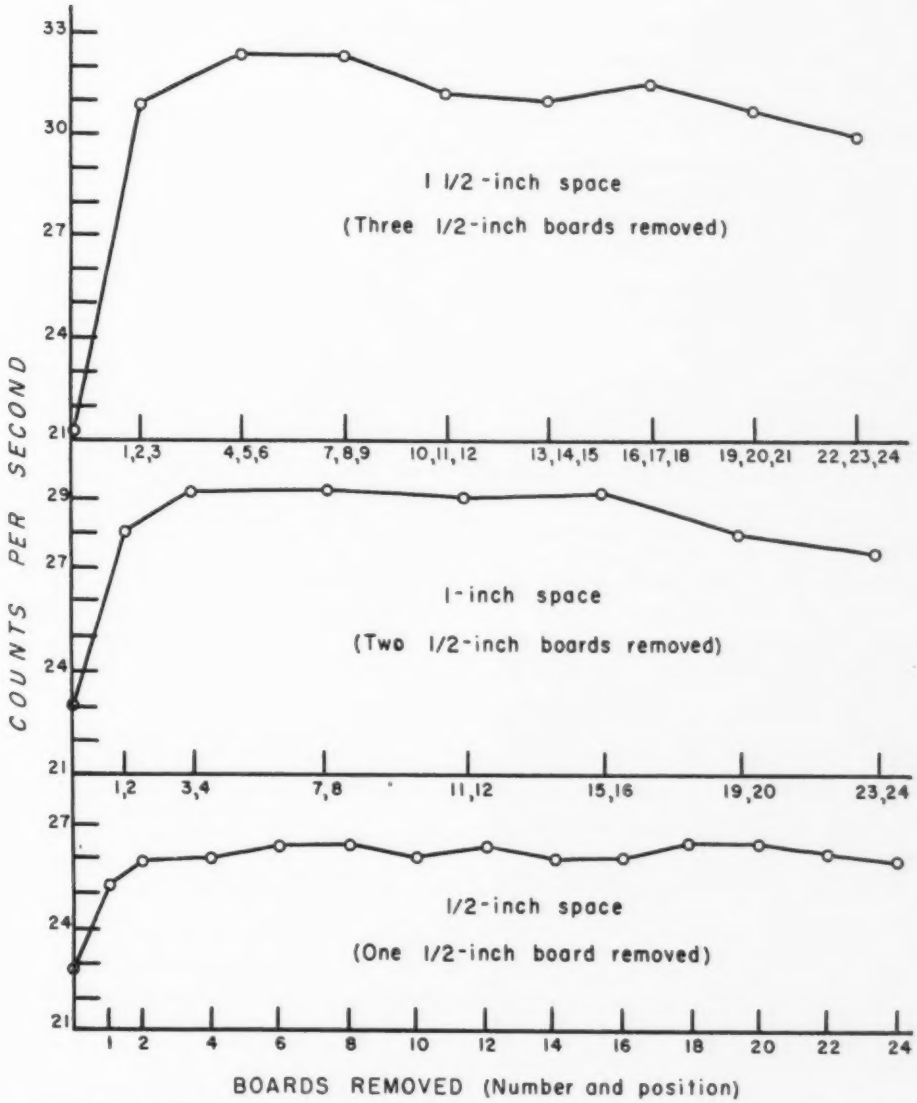

FIGURE 2. *Curves showing resolution of spaces in pile of sugar pine boards at various positions using Sn 113 x-ray of 23 Kev.*

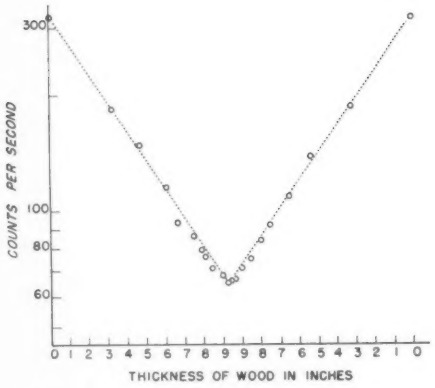

FIGURE 3. *Absorption curve for a black oak log made with a scintillation spectrometer using Ce 144 gamma ray of 135 Kev.*

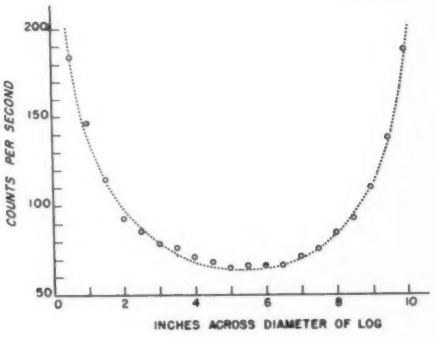

FIGURE 4. *Absorption curve for a black oak log made with a scintillation spectrometer using Ce 144 gamma ray of 135 Kev.*

between a gamma ray source and the detectors (scintillation spectrometer and G-M counter circuit) and measurements made through their cross sections at ½-inch intervals. Both sound and defective logs were measured in this manner.

Because of the circular shape of the log, the absorber could not be increased or decreased in thickness by even increments as all previous absorbers were. Instead, thickness measurements were made every ½-inch across the diameter of the log. At each interval, intensity of radiations was measured. When plotted on semi-logarithmic paper these data show that the results of the attenuation of gamma rays by a circular shaped absorber also form a straight line absorption curve as did those curves when conveniently shaped boards were used (Fig. 3).

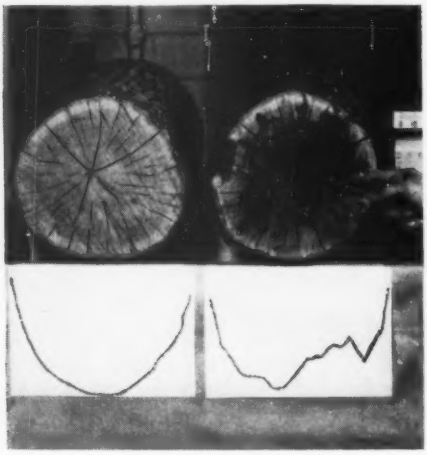

FIGURE 5. *A solid and a defective log shown with their respective absorption curves. (Ohio State University photo.)*

The data used in the construction of Figure 3 were then plotted on linear graph paper. The only difference in the graphs was that the count rate was plotted against the respective distances across the diameter of the log, instead of the thickness measurements every ½ inch across the diameter of the log (Fig. 4). In this manner the defects, if present, would be better illustrated, appearing as conspicuous "dents" in what otherwise would be a nearly semi-circular curve (Fig. 5). The slight variations in the linear curve are probably due to the fact that the log was not perfectly circular, or to the irregularities of the bark on the log.

By using the same geometry that was used in the previous experiments, absorption curves were made for the same black oak logs with the G-M counter circuit and

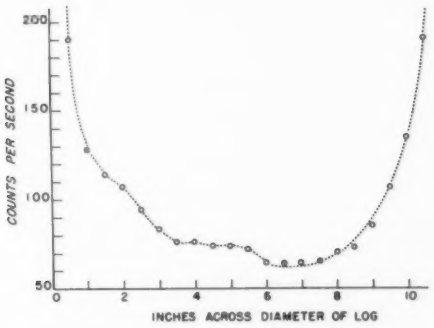

FIGURE 6. *Absorption curve for a black oak log with no visible hole made with a scintillation spectrometer using Ce 144 gamma ray of 135 Kev.*

Ce 144 radiations. These curves indicate that the detection of a defect in the thicker portions of the tree would be more difficult when using a G-M counter circuit than when using a scintillation spectrometer. This is especially important because most defects in trees are near the center.

Another apparently solid oak log was similarly analyzed and an absorption curve drawn (Fig. 6). There was a defect in the log which was not seen until the data were graphed. Upon closer examination, a portion of the log was found to be partially decayed, and hence less dense than the wood surrounding it.

Effect of free water. Having established that holes in wood could be detected by the attenuation of gamma rays, the next question was: would the presence of moisture or free water in these hollow spaces interfere with the detection process?

A black oak log, 3 feet long and approximately 10 inches in diameter, with a hole in one end was chosen as the absorber to be used in these tests. The solid end was sealed with hot paraffin to prevent water leaking out. A *Ce* 144 source was used which emitted a gamma ray of 135 Kev. The source and the collimated scintillation crystal were mounted 3 feet from the floor and 3 feet apart.

The first of the three experiments consisted of moving the sealed log, with no water in its cavity, between the source and the crystal. Measurements of the intensity of radiations were made every ½ inch across the diameter of the log. When the results are plotted on linear paper, the cavity in the log is clearly defined, and even decayed portions which were not visible were also defined (Fig. 7).

The second experiment consisted of moving the sealed log, with its cavity filled with water, between the source and the crystal and making measurements every ½ inch across the diameter of the log. The geometry was exactly the same as in the previous experiment. In this instance the cavity is not readily defined, although some irregularities are shown (Fig. 8).

The third experiment consisted of moving the sealed log, with the water emptied from its cavity, between the source and the crystal and measurements were made every ½ inch across the diameter of the log. Again the same geometry was used. Even though the sides of the cavity in the log were wet, it is clearly defined (Fig. 9). It has been shown, then, that decayed portions or cavities in a log can be detected by means of the attenuation of gamma

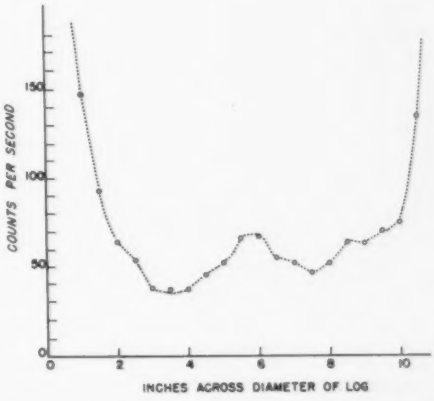

FIGURE 7. *Absorption curve for a black oak log with a visible hole made with a scintillation spectrometer using Ce 144 gamma ray of 135 Kev.*

rays, when using a scintillation spectrometer, but, when the cavities in the log are filled with water, they would be difficult to detect by these means.

Film experiments. A series of experiments were performed using film as the detector of radiations to find defects in the same two black oak logs that were used in the previous experiments. However, this method was discarded because neither the position nor the size of the defect could be precisely determined with one exposure.

Moisture experiments. In all previous absorption experiments with wood boards, the wood used had a constant moisture content for any one absorption curve. Moisture content, however, is not always constant throughout the thickness of the tree. Experiments were, therefore, conducted to find out how differences in moisture content affect the attenuation of gamma rays in wood. Nine small blocks of each of the three species were tested at eight different moisture contents.

It was found that the values of the mass absorption coefficient decreased with an increase in the moisture content of the three species of wood studied. It was also shown that there was little change in the values of the mass absorption coefficient in the species of wood studied with like changes in moisture content. There was very little change in the relative intensity of penetrating radiations through wood

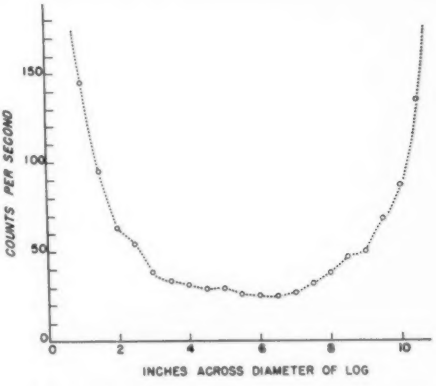

FIGURE 8. *Absorption curve for a black oak log with visible hole filled with water made with a scintillation spectrometer using Ce 144 gamma ray of 135 Kev.*

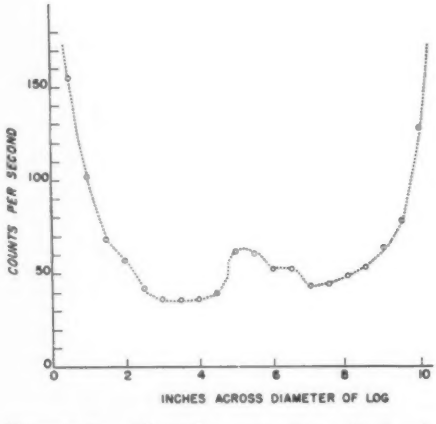

FIGURE 9. *Absorption curve for a black oak log with surface of visible hole soaked with water made with a scintillation spectrometer using Ce 144 gamma ray of 135 Kev.*

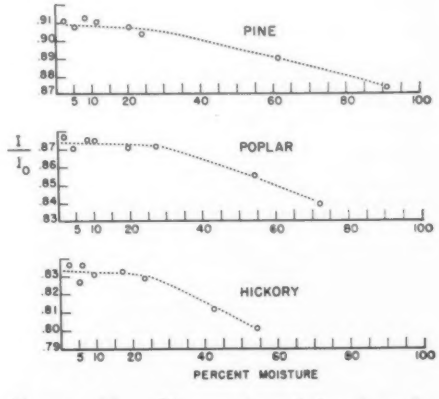

FIGURE 10. *Changes in relative intensity through 1 Cm of pine, poplar, and hickory respectively with changes in moisture content using Sm 144 + n x-ray of 38 Kev.*

from 0 percent to 30 percent moisture content, because of the little change in the density of the wood. Above 30 percent moisture content, there was a greater change in the relative intensity in the denser species of wood than in the less dense species of wood with like changes in moisture content (Fig. 10).

Conclusions

The results of this set of experiments lead to the following conclusions:

1. Decay in wood can be detected by means of the attenuation of gamma rays.

2. The size of such a defect can be determined, regardless of its location, by these means.

3. It appears that radiation energies between 23 Kev for low-density woods and 135 Kev for high-density woods would be the most suitable energies to use to detect these defects.

4. The scintillation spectrometer appears to be the most suitable radiation detector for detecting defects in logs.

5. Variations in the moisture content of wood appear to vary the rate of attenuation of gamma rays by wood, but the mass absorption coefficient of water is less than that of dry wood; therefore, the degree of attenuation is less than that indicated by the percentage variations of the moisture content of the wood.

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Report of For. Comm., New South Wales. 1955. Report of For. Comm. (*In* For. Abs. 16 (4): 594. Oct. 1955).

Variation in Measurements of Light Intensity Under Forest Canopies

BY
GORDON E. GATHERUM

IN A RECENT STUDY concerning the effect of light intensity and soil moisture on the establishment, survival and growth of underplanted coniferous seedlings in stand conversion practices in Iowa, the author evaluated the variation obtained in light readings taken with a Weston Illumination Meter—Model 756 at seedling height under an 80-year-old upland oak understory forest canopy (Table 1). As a guide to future investigators of the light factor, the magnitude of the variation and the number of measurements needed to obtain a given reliability at an acceptable probability level, are presented.

Twenty-five readings were taken at mechanically spaced intervals in each of 4 1/20-acre plots within each of 3 replications between 11 am and 1 pm at irregular intervals during the summer of 1956. Prior to the initial light measurements, the 4 plots within each replication received one of the following treatments: all overstory and understory stems clearcut; all overstory and two-thirds of the understory stems cut; all overstory and one-third of

The author is Associate Professor of Forestry, Iowa State University, Ames, Iowa. Manuscript received Oct. 3, 1960.

TABLE 1. Description of vegetation on the experimental area.

Natural stand

Overstory
Dominant species:
- Northern red oak (*Quercus rubra* L.)
- White oak (*Quercus alba* L.)
- Northern pin oak (*Quercus ellipsoidalis* E. J. Hill)

Stand density (basal area per 1/20-acre):
- Before treatment—3 sq. ft.
- After treatment—0

Average height (feet):
- Before treatment—75
- After treatment—0

Understory
Dominant species:
- Hazelbrush (*Corylus americana* Walt.)
- Dogwood (*Cornus alternifolia* L.)

Stand density (stems per 1/20-acre):
- Before treatment—1,200
- After treatment
  - Clearcut—0
  - Two-thirds cut—400
  - One-third cut—800
  - Check—1200

Average height (feet):
- Before treatment—15
- After treatment—15

Underplanted seedlings

Species:	Age class:	Height (inches):
European larch (*Larix decidua* Mill.)	2-2	8 to 10
Red pine (*Pinus resinosa* Ait.)	2-2	8 to 10
Scotch pine (*Pinus sylvestris* L.)	2-1	6 to 8
Eastern white pine (*Pinus strobus* L.)	3-0	10 to 12
Norway spruce (*Picea abies* L.)	3-0	8 to 10

TABLE 2. Variation in measurements of light intensity under forest canopies.

Plot treatment	Mean (foot candles)	Standard error (foot candles)	Reliability (percent)	No. observations per plot needed to attain reliability within 10 percent of the mean		
				68 percent probability	95 percent probability	99 percent probability
Clearcut	5,111	±598	11.7	34	136	204
Two-thirds cut	1,527	±433	28.4	201	804	1206
One-third cut	1,561	±446	28.6	204	816	1224
Check	548	±187	34.2	292	1168	2620

the understory stems cut; and all overstory and none of the understory stems cut (Table 1). Readings were taken on clear days only, and the sequence of the measurements was alternated to reduce the effect of changes in the relative positions of the earth and sun with time.

The reliability of the readings was greatest in the clearcut plots and decreased rather markedly with an increase in understory density (Table 2). Even though the photoelectric cell was oscillated back and forth to obtain an average reading of the alternate sun-shade spots, variation in the areas containing understory vegetation was considerably higher than in the clearcut plots (Table 2). To increase the reliability of light readings to within 10 percent of the mean at the 68 percent probability level, an additional 9 readings per plot would be necessary on the clearcut plots, 176 on the two-thirds cut plots, 179 on the one-third cut plots and 267 on the uncut plots. At the 99 percent probability level, readings per plot would increase from 204 for the clearcut plots up to 2,620 for the uncut plots (Table 2).

Symposium on Forest Types and Forest Ecosystems

Silva Fennica 105, 142 pp., Helsinki, 1960.

Review by R. Stahelin
U. S. Forest Service

This issue of *Silva Fennica* is devoted to 18 papers by authors from 11 countries (all except the German or French in English) presented at the symposium on forest types and forest ecosystems during the 11th International Botanical Congress at Montreal, August 24, 1959. The purpose of this symposium was to discuss the prospects of finding a common platform for the different schools of forest typology. J. S. Rowe (Canada), summarizing the discussion of these papers, stated that a common basis is found in the basic concept of ecosystems (Tansley) and biogeocoenosis (Sukachev). Ecosystems are geographic units and should be systematized with reference to the earth's surface. Classification should be based both on forest vegetation and forest sites. The purpose of use determines which system of typology should be used, provided that a common conceptual basis is accepted. Conclusions of the discussion were presented at the Fifth World Forestry Congress in Seattle in a paper entitled "The Ecosystem Concept in Forestry" by the joint authors, J. S. Rowe, P. G. Haddock, G. A. Hills, V. J. Krajina, and A. Linteau.

An Electronic Dot Counter

Equipment Note by Reid M. Kenady
Weyerhaeuser Forestry Research Center
Centralia, Washington

Methods of determining area from a base map include the use of various planimeters, and the area dot grid such as described by Bryan[1]. The dot grid is widely used because it is simple and low in cost. However, prolonged, continuous counting by this method can prove so fatiguing as to increase the likelihood of mistakes in counts. Here the use of an electronic counter with dot grid can reduce fatigue, uncertainties, and errors. This note gives the description of a readily improvised electronic counter, and discusses its use for area determination.

The dot counter which is used with a grid to measure area, consists of an assembly of a transformer, an electric counter and a modified ball-point pen. Figure 1 shows the wiring diagram for the complete assembly, and a cross section of the pointer. A single-pole toggle switch (2) is mounted between the power supply and the 24-volt transformer (1). The transformer is a product of the Edwards Company (their No. 898). The 24-volt counter (Model MDB-S4-115A) (3) is a product of Mercury Controls Division and so listed in radio and electrical parts catalogs. It is designed for panel mounting and can be mechanically reset to zero with a single turn of a knurled knob. In the prototype model, the transformer was housed in a 3 by 3 by 3 inch, ¼-inch plywood box with the counter mounted on the box at an angle of approximately 30 degrees for reading convenience. A light, flexible hook-up wire (4) connects the counter to the pointer, which is a modified Paper Mate ball-point pen. The pen is cut at the pocket clip to permit installation of the counting mechanism.

[1]Bryan, Milton M. Area determination with the modified acreage grid. J. For. 41: 764-766. 1943.

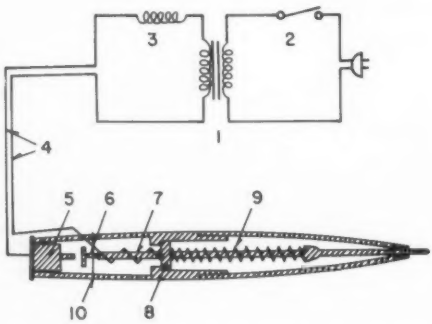

FIGURE 1. *Diagram of Electronic Dot Counter:* 1, *transformer*; 2, *switch*; 3, *counter with coil*; 4, *leads to pointer*; 5 *and* 6, *pointer contacts*; 7, *pen filler*; 8, *plastic centering ring*; 9, *spring*; 10, *cut at clip position.*

Parts 5 and 6 are contacts that close the circuit to activate the counter. The stationary contact (5) is a portion of the thumb release placed in the top of the pen (10). The moving contact (6) is a copper flathead nail inserted into the pen filler (7). A lead wire, which serves as a part of the electrical circuit but does not restrict movement, is loosely wrapped around the top of the filler. After each contact the filler is returned to its no-contact position by the spring (9), which is contained and held in compression between the plastic ring (8) and the lower part of the filler, which is pinched to form a shoulder. The spring is installed so that a light pressure on the pointer closes the contacts. They are separated by approximately 1/16-inch. The top of the pen is glued or taped in place when the assembly is completed.

The electronic counter is being used with an area dot grid to determine the size of land units mapped in a recent soil survey. The grid is placed at random over a selected soil type and the pointer is depressed on each dot occurring within the unit. Action of the pointer is positive and rapid. The number appearing on the counter is equal to the number of acres in the area when a one-dot-per-acre grid is used. Used in this manner, the dot counter has facilitated accurate counts on areas totaling 300,000 acres. It is most useful when counting dots in a large unit.

Several counting devices have been patented which are similar in principle to the one de-

scribed here but differ in their application[2]. A special instrument for area calculation using an automatic counter is available from the Martin-Kuykendall Company of Albuquerque, New Mexico. Counters ranging from the elaborate to the simple design described here should find many uses in the field of forestry. Counters might be used in conjunction with aerial photographs from which various tree counts are made. A modification of the pointing device could simplify the job of counting seeds. Wherever routine and tedious counting tasks occur, a counter could probably be adapted to simplify the work.

[2]Kavanagh, Frederick W. Apparatus for counting bacterial colonies. U. S. Pat. No. 2,548,478, April 10, 1951. Fulboam, E. G. Indicating instrument. U. S. Pat. No. 2,511,202, June 13, 1950. Mast, G. M., *et al.* Dot counters. U. S. Pat. No. 2,875,950, March 3, 1959.

Inexpensive Ring Analyzer for Cumulative Summerwood Measurements

Equipment Note by R. M. Echols and Alvin B. Bowden
Southern Forest Experiment Station

The ring analyzer shown in Figure 1 was constructed at the Southern Institute of Forest Genetics, Gulfport, Mississippi, to facilitate measurement of ring width and percent of summerwood in increment cores. It permits faster work than is possible with vernier calipers with less accumulative error. Radial strips as well as large or small cores can be accommodated. Using a standard stereoscopic microscope with a choice of magnification, one can use the scale to measure single rings or accumulate widths of summerwood for the entire sample. If desirable, a vernier might be added to the scale.

The following staining schedule produces strong color differentiation in spring- and summerwood of southern pines, particularly if the cores are allowed to surface-dry before measurement:

Soak cores for 3 days in 0.5 percent solution of phloroglucinol in distilled water

Transfer to a 10-percent solution of hydrochloric acid in distilled water and soak for 2 days

Rinse and store in tap water until measured.

An india ink reference dot is placed on the under lens of one of the microscope eyepieces.

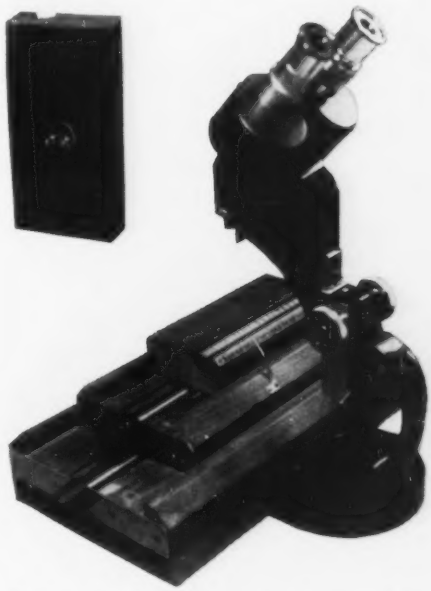

FIGURE 1. *Ring analyzer on microscope base, ready for use. Inset at upper left shows slotted nut on underside of core carrier.*

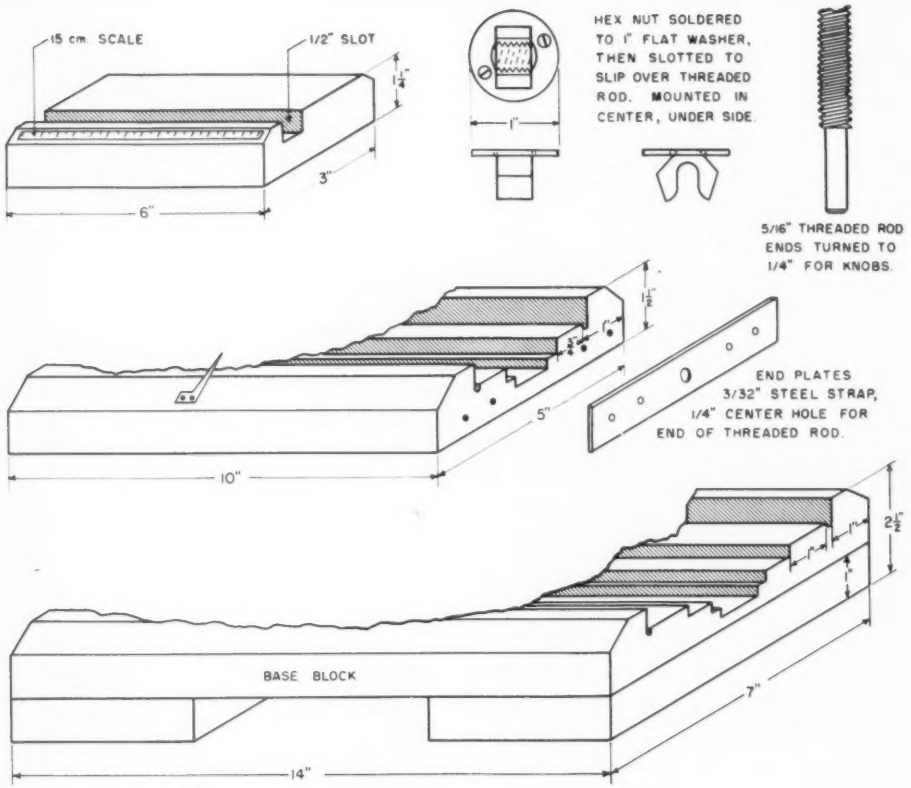

FIGURE 2. *Construction details of the ring analyzer.*

The operator zeros the scale, aligns the dot with the left end of a core, then moves the core past the dot, using the upper knob to traverse the summer wood only and the lower knob for all other movements. The accumulated summerwood is read in mm. and may be recorded along with total core length.

Figure 2 shows construction details. Any species of even grain, well-cured wood may be used. The 5/16-inch threaded rods are available at hardware stores; knobs are No. 3 one-hole rubber stoppers. In addition to facilitating alignment, the slotted nuts allow the slides to be lifted and returned to starting position faster than by turning the knobs. It is estimated that the ring analyzer can be constructed at a total expenditure of two man-days and two dollars for materials.

Stem Elongation and Time of Cone Initiation in Southern Pines

BY
WILLIS A. EGGLER

KNOWLEDGE of the calendar time of pine cone formation is important in forest genetics. Both forest geneticists and practicing foresters are interested in stimulating cone production, at the earliest possible age on young trees, and in increased quantity on older trees. Treatments designed to increase cone production promise little unless applied before the time at which initiation of cone primordia may be expected.

During the past three years a study of the phenology of southern pines growing in Louisiana and Mississippi has been in progress, involving both vegetative and reproductive structures and processes. Some observations on stem elongation and on the probable times of cone initiation have been made as a part of the large study. These subjects are treated together because stem elongation bears directly on cone initiation. In all instances observed both microsporangiate (male) and megasporangiate (female) cones have been initiated only on the last stem growth of the year.

Pattern of Stem Elongation

In temperate and cold climates a woody stem usually undergoes one phase of elongation from one terminal bud each year, but exceptions to this are not uncommon and instances of renewed activity of subsequent terminal buds, after growth has normally ceased, have been reported. The term lammas shoot has been applied to this type of growth when it occurs late in the season.

Recurrent or intermittent elongation of stems has been discussed by several persons. Doak (1935) reported that longleaf pine (*Pinus Palustris* Mill.) and *P. pinaster* Ait. growing near College Station, Texas, resumed growth after a summer dry-period was followed by rains. Kienholz (1941) reported three maxima of stem elongation in red maple stump sprouts growing in Connecticut. Friesner (1943) found three peaks of growth for leaders and branches of 14- and 15-year-old red pine and eastern white pine trees growing in Indiana. Byram and Doolittle (1950) stated that northern pines complete height growth in six or seven weeks, whereas height growth in southern pines is perodic and a tree may put forth two or more leaders during the growing season which may last five to eight months. They noted a rest period of a month or more between growth periods. Kramer and Kozlowski (1960) reported recurrent flushes of growth taking place in loblolly pine seedlings grown in a greenhouse, with periods of cessation of growth falling between the active periods.

The observations upon which this report is based have led to two main conclusions about elongation of stems of pine trees

In its early stages the project was supported in part by a grant from A. J. Hodges Industries, Inc., Shreveport, Louisiana. Longleaf pine specimens from Many, Louisiana, were collected by T. E. Campbell of A. J. Hodges Industries, Inc.; specimens from the Southern Institute of Forest Genetics, Forest Service, U. S. Department of Agriculture, Gulfport, Mississippi, were furnished by E. Bayne Snyder. More recent aspects of the study carried on near Covington, Louisiana, have been supported by a grant from the National Science Foundation, G-3937. The author is Professor of Botany, Tulane University, New Orleans, Louisiana. Manuscript received Sept. 30, 1959.

growing in southern Louisiana and Mississippi: (1) Elongation of both leaders and branches during a single growing season is usually the result of the elongation of more than one terminal bud. As many as five have been observed to elongate on the leader of a loblolly pine (*Pinus taeda* L.) tree. (2) In nearly all instances when elongation resulted from two or more buds the buds elongated consecutively, not intermittently or recurrently as others have reported. As soon as one terminal bud ceased elongation the next one began and there was no rest period between growth phases. An elongation curve for branch or leader for the entire growing season is therefore nearly always a smooth one and not a fluctuating one with several maxima.

The terms recurrent flushes of growth, recurrent growth, and intermittent growth, used by others, do not accurately describe the pattern of elongation of stems of the pine trees discussed here. The term "multiphase growth" will be used to indicate elongation from two or more terminal buds, each phase being the growth from one bud.

Observations of Stem Elongation From Two or More Terminal Buds

Elongation of stems involving several buds was observed in four species of southern pines: longleaf pine, slash pine (*Pinus elliottii* Engelm.); loblolly pine and shortleaf pine (*Pinus echinata* Mill.). Both large and small trees were observed.

Large trees. One series of observations was made on branches which were collected between August 1956, and February 1957, from two longleaf pine trees growing in the forest of the Southern Institute of Forest Genetics (hereafter referred to as S.I.F.G.). These trees, designated as numbers 3 and 5, were about 14 inches d.b.h. Forty-nine branches with young female cones and 27 which had borne male cones the previous spring were collected from tree 3; 34 branches with young female cones, 22 with male cones, and 5 neutral branches (no cones) were collected from tree 5.

Branches from tree 3 which bore first-year female cones had elongated in one, two, or three phases, with an average num-

TABLE 1. Summary of growth phases (number of successive terminal buds involved in stem elongation) of six pine trees.

Tree	No. of branches	Ave. no. phases per branch	Average length of phases for — Phase 1	Phase 2	Phase 3	Phase 4
			Centemeters			
Pinus palustris						
S.I.F.G. (1956)						
Tree 3						
With ♀ cones	49	1.9	5.9	2.2	2.4	....
With ♂ cones	27	1.4	3.6	2.4	1.0	....
Tree 5						
With ♀ cones	34	2.1	9.3	3.1	1.7	1.5
With ♂ cones	22	1.4	4.2	2.3	2.5	....
Neutral	5	1.4	9.5	4.0	....	....
Slidell, Louisiana (1955) (Ave. 3 trees)						
With ♀ cones	29	2.5	8.9	2.4	1.2	....
Pinus echinata						
Covington Forest (1957)						
With ♀ cones	39	2.7	12.4	5.2	5.3	6.0
With ♂ cones or neutral	60	1.7	10.9	6.1	6.3	5.0

ber of 1.9 (Table 1). Branches which had borne male cones in the spring of 1956 had an average of 1.4 growth phases, and the total elongation for the season was less than for branches with female cones. Some of the branches on tree 5 with first-year female cones had grown in four phases; the average number was 2.1. Branches with male cones averaged the same number of growth phases as similar branches on tree 3—1.4. Neutral branches elongated less on an average, and none had more than two phases.

Twenty-nine branches, all with first-year female cones, were collected from three mature longleaf pine trees growing near Slidell, Louisiana. The branches averaged 2.5 growth phases for the 1955 season, up to July 12, when collected (Table 1). Most of them elongated in either two or three phases.

On April 4, 1958, 99 branches were collected from a shortleaf pine tree ten inches d.b.h., growing about six miles northeast of Covington, Louisiana. (This area will be referred to hereafter as Covington Forest.) At the time it was still possible to identify 1957 stem growth, and 1957 female cones were still attached. It was not possible to determine which branches had borne male cones the previous year. Branches of this shortleaf pine tree also elongated in several phases (Table 1); 39 which had female cones averaged almost three phases, and 60 with male cones, or neutral, not quite two. A few in each group had as many as four growth phases.

From January 1, 1958 to late June 1959, measurements were made, at regular intervals, of the lengths of several branches on three trees in the Covington Forest. Tree number 1 was a loblolly pine, 17 inches d.b.h. which showed 16 growth rings at 4½ feet; tree 11, a longleaf pine, was 21 inches d.b.h. and had 37 growth rings; tree 32 was a slash pine, 16.5 inches d.b.h., and had 32 growth rings. Branches measured were classified as to whether they were primary, secondary, or tertiary. Results are given in Table 2, which shows the number of branches measured in each of several categories.

All branches with male cones, on all three trees, elongated in one phase only; branches with female cones, elongated in two or three phases. Neutral branches usually elongated in one, two, or three phases, but one neutral branch on tree 1 and one on tree 11 failed to grow at all in 1959. It was evident that, on an average, primary branches elongated more, and in more phases, than secondary, and secondary more than tertiary (Table 2). If the total number of growth phases for each category is divided by the number of branches, values as follows are obtained: primary branches—2.67; secondary branches—1.76; tertiary branches—1.32.

A certain trend is evident in the relation between kind of cone and type of branch, also. Primary branches usually bore female cones, if any; secondary bore either female or male, with female in the majority; tertiary branches bore either kind, with male in the majority. If the growth of each branch for each year is considered as a separate unit the total number of units for all three tests is 6 primary, 83 secondary, and 49 tertiary. None of the primary branches bore male cones; 10 secondary, a little over 12 percent, produced male cones; 17 out of 49 tertiary, about 34 percent, had male cones. Four out of 6, or about 67 percent, of the primary branches produced female cones; 44 of the 83 secondary branches, 53 percent, and 12 of 49 tertiary branches, 24 percent, produced female cones.

Wareing (1958) diagramed a tree of *Pinus sylvestris* L. in England in which only male cones are shown on lower branches. At the middle heights female cones are shown on primary branches and on some secondaries, male cones on other secondaries and on tertiaries. Near the top of the tree there are no male cones and female cones are borne on primaries and secondaries. No attempt has been made in the present paper to correlate cone type with elevation on the tree, as Wareing did.

TABLE 2. Growth phases produced by branches of tree No. 1 (loblolly pine), tree No. 11 (longleaf pine), and tree No. 32 (slash pine) in 1958 and 1959. Numbers indicate branches measured in each category.

Primary branches		Secondary branches		Tertiary branches	
1958	1959	1958	1959	1958	1959
		TREE NO. 1			
		With ♂ cones		*With ♂ cones*	
		1 phase 2	3	1 phase 2	2
		With ♀ cones		*With ♀ cones*	
(None measured)		2 phases 2	1	2 phases 4	–
		Neutral		*Neutral*	
		1 phase 3	3	1 phase 2	4
				No growth –	1
		TREE NO. 11			
		With ♂ cones			
		1 phase 2	–		
		With ♀ cones		*With ♀ cones*	
		3 phases 4	–		
(None measured)		2 phases 1	3	2 phases 2	2
		Neutral			
		2 phases 1	1		
		1 phase 2	3		
		No growth 1	–		
		TREE NO. 32			
		With ♂ cones		*With ♂ cones*	
		1 phase –	3	1 phase 4	9
With ♀ cones		*With ♀ cones*		*With ♀ cones*	
3 phases 2	1	3 phases 4	2	3 phases 1	–
2 phases 1	2	2 phases 14	12	2 phases 2	1
		♀ & ♂ *cones*			
		2 phases –	1		
Neutral		*Neutral*		*Neutral*	
3 phases 1	–	3 phases –	1		
2 phases –	1	2 phases 5	–	2 phases 3	1
		1 phase 3	6	1 phase 5	4

But the general relation between rank of branch and the type of cone the branch supports is similar for pines reported in this paper to the one described by Wareing.

Small trees. Young loblolly pine and slash pine trees, 10 to 15 feet tall, grew in abundance in the Covington Forest. Without exception at least some branches on every tree in this size range, examined late in June 1958, had already grown in a multiphase manner during the 1958 season. Six loblolly and 13 slash pine trees were chosen and each branch was examined to determine the number of growth phases added in 1958. Whorls of branches were both primary and secondary—interpreted according to the usage of Wakeley and Marrero (1958), in which the terms are used to indicate if whorls were produced by the first or by later terminal buds of the season. However, each branch was primary in that it came directly from the main axis. The loblolly pine trees were examined between July 1 and 22, and the slash pine between June 27 and July 25, 1958. Growth was mostly completed by that time but some branches may have added another phase. Trees were not the same size and the number of whorls differed, so branches were combined in the

TABLE 3. Number of growth phases produced in 1958 by branches at different levels for 6 loblolly and 13 slash pine trees, 10-15 feet tall. Numbers indicate how many branches at each level elongated in the manner shown.

Location of whorl	Loblolly pine by growth phases				Slash pine by growth phases			
	0	1	2	3	0	1	2	3
Top whorl	--	5	6	5	--	14	24	--
2nd from top	--	3	8	4	--	10	19	7
3rd from top	--	3	10	2	--	12	11	1
3rd above middle	--	6	2	--	--	1	7	--
2nd above middle	--	2	3	--	--	3	3	1
1st above middle	--	15	3	--	--	18	19	--
1st below middle	--	12	2	--	--	15	10	--
2nd below middle	--	6	--	--	--	3	2	--
4th from bottom	--	9	--	--	--	12	--	--
3rd from bottom	2	8	--	--	2	25	1	--
2nd from bottom	4	10	--	--	3	29	--	--
Bottom whorl	4	5	--	--	12	20	--	--

manner indicated in Table 3, top whorl, second from top, and so on.

In general the number of growth phases is lowest in the lowest branches and it increases progressively upward. Branches in the top whorl produced the greatest number of phases in the case of loblolly pine, while in slash pine it was the whorl second from the top. The average number of phases for each of 139 branches measured on the six loblolly pine trees was 1.3, as was also the average for 285 branches on 13 slash pine trees. The fact that a number of lower branches failed to elongate reduced the average appreciably.

The actual amount of elongation of the branches of the young pine trees is not reported here but it can be stated that total growth of each stem was approximately proportional to the number of consecutive buds contributing to the elongation (growth phases), and upper branches grew more than lower.

Friesner (1943) pointed out that in the case of small pine trees growing in Indiana elongation of both secondary and tertiary axes decreased from the top downward. He noted two possible causes for this decrease. One is that lower branches are farther from terminal buds where growth-initiating substances are produced. The other is that food reserves for cambial activity are used faster in the lower part of the tree where the cambial cylinder is largest.

Consecutive Periods of Stem Elongation More Common Than Recurrent

Evidence for consecutive, rather than recurrent, periods of growth was found in measurements of elongation of main stems and branches of trees in the Covington Forest. Most measurements reported are for 1958 growth.

Apical growth of nine pine trees (four loblolly, one longleaf, and four slash pines) in a height range of from 12 to 20 feet was recorded. The height growth pattern was as follows: two trees each elongated in five phases (from five buds) and there was no resting period between phases; one tree elongated in four phases and there was a time interval between phases three and four; another elongated in three, without any time break between; another in three and there was a break between two and three; the other four each elongated in two phases without any cessation of elongation between them.

During the same time growth of 144 branches on 11 trees, including the nine above, was measured. The branches were

largely secondary and tertiary. Eleven branches elongated in three phases and in none of them was there a rest period; 57 branches grew in two phases and in only four of them there was a time break between the two phases; the other 76 branches elongated from one bud only. In all instances where there was a rest period it came just before the last phase. A more complete record of stem growth in the above trees, including that for 1959, will appear in another paper.

Growth in length of a woody stem in consecutive phases has apparently not been reported before. Kramer and Kozlowski (1960) state that "no matter how favorable the environment, woody stems do not grow continuously . . ." They cite several possible causes of dormancy or growth cessation between periods of growth. These causes include accumulation of inhibitors, unfavorable temperature, and deficiency of nutrient. In instances reported in this paper where there was no period of dormancy it is obvious there could have been no growth inhibitor effect. It is probable that for trees in this study a deficiency of food or of growth substance, or of both, was a cause of growth cessation. When there was a break between growth phases it came just before the final growth, near the end of the growing season, when nutrient or growth substance might no longer be adequate.

Time of Cone Initiation

Mergen and Koerting (1957) summarized reports of time of cone initiation for various conifers. In the present report only a few particularly relevant records will be cited. Duff and Nolan (1958) reported that in *Pinus resinosa* Ait., growing near Chalk River, Ontario, cones began to develop about August 15th and were identifiable by the end of August. Mergen and Koerting (1957) examined slash pine trees growing near Lake City, Florida, and concluded that male cones started about June 25th, and continued to initiate for about six weeks. The earliest female cone was found in late August. The authors believe the female cones are initiated during a two-week period.

In the present study three procedures have been used to determine when cones are initiated: (1) microscopic examination of sections of buds presumed to have cone primordia; (2) examination of two lots of buds from each of three trees, collected on different dates during the time when cones may be initiated—the "mass collection" method; and (3) removal of buds which might be expected to produce female cones.

Bud sections. At the outset it was hoped that it would be possible to use bud sections to determine rather precisely when cones are initiated, but such was not the case. Primordia of male cones, female cones, short shoots, and branches are not morphologically distinct in the earliest stages. Not until the bud had developed considerably was it possible to identify the different elements; then it was done on the combined evidence of structure, position, and number of each type of element present.

Mergen and Koerting (1957) refer to "—sectioning blindly—" until cones are big enough to see in dissection. To date no cone has been positively identified in a microscopic section if it had not been seen previously during dissection under a binocular dissecting microscope. This was not realized for some time and scores of buds have been sectioned "blindly" without results. The microscopic section is useful to verify what was suspected from the dissection. It also permits detailed study of cone primordia.

Results from the sectioning method have not been particularly satisfactory to date. The number of specimens examined during the critical time was small. Only one or two buds were collected each week, so that the supply on a single tree would last for a year or more to permit study of an entire annual cycle. Up to the time when it becomes possible to detect the presence of cones without first dissecting, the odds in favor of having a bud with cone primordia are not very great. It is hoped that examination of more terminal buds may

TABLE 4. The earliest dates on which cone primordia have been identified in microscopic sections of buds.

Location	Species of pine	Tree no.	Kind of cone	Date
S.I.F.G.	Longleaf	1	Female	10/31/55
S.I.F.G.	Longleaf	3	Male	8/ 6/56
			Female	10/ 8/58
S.I.F.G.	Longleaf	5	Female	7/30/56
Many, La.	Longleaf	1-7	Female	7/22/55
Covington, La.	Longleaf	11	Female	10/12/58
Covington, La.	Longleaf	12	Male	10/ 8/58
			Female	10/ 8/58
Covington, La.	Slash	29	Male	7/31/58
Covington, La.	Slash	32	Male	8/27/59
			Female	9/25/57
Covington, La.	Loblolly	2	Male	10/29/58
			Female	10/15/58

reveal some cone primordia at dates earlier than those given in Table 4, which represent the earliest dates on which cone primordia were definitely identified in sections from buds from several different trees. Further findings will be included in another report.

The earliest record in this study for primordia of male cones on longleaf pine is August 6; female cones were found in the latter part of July. These were from different places and in different years.

The first record for primordia of male cones on slash pine is July 31, and for female cones, September 25. Primordia of male cones on loblolly pine were found on October 29, and of female cones, on October 15.

Mass collections. A healthy cone-producing tree of each of three species of pines was selected in the Covington Forest. The slash and loblolly pines were trees from which no collections had been taken nor measurements made. The longleaf pine was tree number 12, from which some buds had been collected. The method used was to collect a number of buds from the east half of the tree on one date, and then after a few weeks a number of buds from the west half of the same tree. This was a "blind" procedure and there was no particular significance in the choice of dates for collecting. Buds were collected from the slash pine on August 8 and October 1, 1958; from the longleaf on September 6 and October 8, 1958; from the loblolly on August 15 and October 15, 1958. In the first collection of slash pine made on August 8, tertiary branches were collected along with primary and secondary branches, but in subsequent collections no tertiary branches were included. Buds were examined for cone primordia under a binocular dissecting microscope.

Table 5 indicates that for the particular trees concerned cone primordia were rather late in reaching a stage for identification. A few slash pine cones of both types were recognized in the first collection, but no

TABLE 5. Incidence of cone primordia in buds collected from branches of three pine trees.

	Date collected	No cone primordia found	With ♂ cone primordia	With ♀ cone primordia
Slash pine				
82 primary, secondary and tertiary branches	8/8/58	67	11	4
36 primary and secondary branches	10/1/58	10	11	15
Longleaf pine				
43 primary and secondary branches	9/6/58	40	3	0
45 primary and secondary branches	10/8/58	12	10	23
Loblolly pine				
68 primary and secondary branches	8/15/58	68	0	0
34 primary and secondary branches	10/15/58	4	9	21

loblolly cones were found. In 43 longleaf pine buds no female cones were identifed and only a few male cones were found. However, in October approximately half of the buds collected from the longleaf pine tree, a little less than half from the slash pine, and considerably more than half from the loblolly, had female cones.

These results suggest that, in 1958 at least, cones were initiated during a period of several weeks, running to early September. In the trees examined slash pine cones developed earlier than those of loblolly pine. The first longleaf pine collection was not made until September 6, so it is difficult to compare that species with the other two. However, the absence of female cones from the September 6 collection and the tremendous increase during the next month indicate that the longleaf pine cones developed rather late.

Debudding. Terminal buds follow very much the same pattern of development in the several kinds of pines studied. After a branch has undergone its phases of rapid elongation in the spring and early summer the terminal bud gives rise to the primordia which will emerge the next spring, and it enlarges considerably, particularly in August and September. At the bases of buds which terminate many of the primary and secondary branches, branch-buds (which will elongate into branches the next spring) are visible by middle and late August. Female cones, when present, are near the apex of the bud, above the branch buds. Branches do not normally produce cones the same year they emerge from buds. To test the possibiilty of altering this, several buds which terminated primary and secondary branches, buds which most probably had primordia of female cones started, or about to start, were cut off just above the branch buds. It was assumed that the terminal bud would not regrow but that there might be a possibility of inducing cone initiation on the new branches.

Buds of 12 primary or secondary branches near the top of tree 32 (slash pine) were cut off, in the manner indicated, on August 21, 1958. On September 6 buds terminating 12 primary or secondary branches on tree 1 (loblolly pine) were similarly removed.

As was expected, branches grew from the bases of nearly all of the buds the next spring. One new branch on a primary branch of tree 32 produced two normal female cones. They were ready for pollination in mid-February 1959, along with the other female cones on the tree. It is reasonable to assume that these two cones were initiated after August 21, when the terminal bud was removed. It follows that if it is possible for cones to be initiated in branch buds that late in the season then it may be possible in terminal buds also.

Saito (1957) has reported that when several treatments, including manuring, pinching, shoot pruning, and root pruning, were used in an attempt to find a means for control of sex differentiation in Japanese red pine and black pine strobiles, that only pinching resulted in sex transition to female. By pinching at certain times male strobiles, branch primordia, and even dwarf shoots below the part pinched off developed into female strobiles. Saito did not give an explanation for the sex transition but he did report that spraying with 10 ppm naphthaleneacetic acid gave rather similar sex transition. The implication is that pinching altered the growth substance balance in the stem just below the region of pinching. It is reasonable to assume that a similar explanation applies to the slash pine branch discussed above.

The three types of observations just discussed seem to indicate that the season during which cone development may begin may be much longer than has generally been suggested. It is believed that female cones of longleaf and slash pines were first initiated in early July because a few were identifiable by late July or early August. The evidence from the second and third procedures seems to indicate that cones continued to start in longleaf and slash pine any time thereafter, until almost the end of August.

It was pointed out earlier that development of the elements, including cones, in the terminal bud occurs after rapid elongation is completed. Branches sometimes do not complete their rapid elongation until about June 15, and hence cone initiation takes place after that time. All the observations indicate that much cone initiation takes place late in the season.

Steinbrenner, Duffield, and Campbell (1960) reached the conclusion that primordia of Douglas-fir are labile. Applications of fertilizer made after primordia were presumed to have been determined resulted in an increase in cone production.

Summary

Multiphase growth of stems, a condition in which successive periods of elongation from successive buds takes place during a growing season, is common among pines growing in Mississippi and Louisiana. This is not only early season growth, followed by renewal of growth late in the season if moisture and temperature happen to be favorable, but rather a series of elongations, usually consecutive, in spring and early summer. Growth of stems by elongation of consecutive buds was observed in mature trees of longleaf, slash, loblolly, and shortleaf pine. Branches elongated in from one to four phases. Branches on young trees also usually elongated in a multiphase manner. Several loblolly and slash pine trees 10 to 15 feet tall were examined and branches were found to have elongated in 0, 1, 2, or 3 phases in 1958.

Three different procedures were used to obtain information about the time when cones are initiated. One or two buds were collected each week from each of several trees. The buds were dissected, fixed, embedded, and sectioned. To date this method has added very little to information already in the literature. The earliest dates on which cones have been identified are: longleaf pine female cone—July 22, longleaf male cone—August 6, slash pine male cone—July 31, slash pine female cone—September 25, loblolly female cone—October 15, loblolly male cone—October 29.

Looking for the earliest cone is partly a game of chance and is believed to have less value than a method which indicates when the main mass of cones is initiated. The "mass collection" method furnished some information in this direction. A number of buds were removed from one side of a tree for examination for cone primordia, and a second collection was made from the other half of the same tree at a later date. A comparison of the cone yield in the two collections indicates when most of the cones form. For two trees (one slash and one loblolly pine) the great majority of female cones reached a recognizable stage after the middle of August; for a longleaf pine female cones became recognizable after September 6. Male cones developed a little earlier. Remembering that occasional cones may be recognized in late July, it follows that the overall period during which female cones initiate must be about two months long, most of July and all of August.

A third technique corroborated the conclusion reached from the second. About 12 primary or secondary buds on each of two trees were cut off just above the base of each bud. A slash pine was debudded on August 21; a loblolly pine on September 6. One branch growing from the base of one of the slash pine buds produced two female cones in 1959. This was the first instance witnessed in which a branch produced female cones in its first year. This phenomenon is interpreted to be the result of the removal of the end of the bud, and it follows that the cones were initiated after August 21, the date of debudding.

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Loblolly Pine

By W. G. Wahlenberg. School of Forestry, Duke University, in cooperation with forest industry and the Forest Service, U.S. Department of Agriculture. Seeman Printery, Inc., Durham, N. C. xxii plus 603 pp., illus. 1960. $7.

Review by Philip C. Wakeley
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In timeliness, content, organization, emphasis, and format, *Loblolly Pine* sets a standard hard to equal and almost impossible to surpass. Wahlenberg's style is perhaps studiedly varied, but prevailingly terse, vigorous, and clear. The frontis-piece and 11 photographic plates, while not outstanding, are well selected and of acceptable quality. A few of the 116 figures require some puzzling over, but most are ingeniously executed with a force and simplicity that give them an almost poster-like impact. All these things make for easy reading —fortunately, as the book will have to be read repeatedly by most foresters in the South and by many elsewhere.

The 12-page introduction is followed by nine chapters on the species and its environment, protection, natural regeneration, artificial regeneration, growth and yield, management of immature timber, management of mature timber, management for other purposes (including water, livestock, and wildlife), and properties and uses. Except for that on other uses (29 pages), these longer chapters include from 44 to 68 pages apiece. The 21-page appendix presents 13 tables carefully selected for maximum usefulness in intensive management of loblolly pine, the U.S. Forest Service interim log grades for southern pine, an adroitly annotated list of 46 insects attacking loblolly pine or its products, and a similar list of 45 pathogenic and wood-destroying fungi, together with the names of the fungi known to form mycorrhizae on loblolly roots. The 70-page bibliography cites a great part of what the preface aptly describes as the essential but widely dispersed and inaccessible literature on the species. (In this connection,

school heads, station directors, industry executives, and journal editors should take to heart the second full paragraph on page xi.) An index of authors and an excellent subject index complete the volume; in each index the text, figure (or plate), and table references are helpfully distinguished by Roman, boldface, and italic type, respectively.

Each of the ten chapters concludes with a ½-page to 4-page summary. To start by reading these ten summaries is to marvel at the completeness, clarity, and assurance with which the author has described *Pinus taeda* L., its environment, its management, and its uses, in a mere 25 pages.

Insight into the genesis of the summaries increases with reading of the text as a whole. Comprehensive historical background and painstakingly gathered, sifted, and collated technical details are all there, and all superbly documented. Organization, emphasis, and conclusions bear the mark of Wahlenberg's long career in research and publication, including some 30 years of work at the Southern and Southeastern Forest Experiment Stations, and of his experience in monographing longleaf pine.

Full appreciation of summaries and main text, however, requires some analysis of the 1494 titles in the bibliography.

Such an analysis at once corrects certain careless assumptions that (because he wrote the book mainly at Asheville and Durham) the author may have injected a northeasterly bias into his discussion.

Wahlenberg cites only five of his own previous publications. Bibliographically, he has relied mainly on 20 authors from Ashe to Zahner, seven of whom have worked primarily at the Southern Forest Experiment Station, eight at the Southeastern, and one (like Wahlenberg himself) at both. Among them, the 20 contribute 345 titles—more than 23 percent of the whole bibliography. The individual author contributing the most titles and cited on most pages is Reynolds of the Southern Station. In all, papers by some 114 Southern Station workers are cited. Clearly the western part of the loblolly range has not been overlooked.

In fact, little if any pertinent information seems to have been overlooked.

The bibliography cites the names of 532 individuals in addition to the twenty listed above and to various organizations and the inevitable "Anonymous."

Material is drawn not only from federal and state forestry publications and from forestry, forest products, botanical, entomological, and pathological periodicals and the proceedings of academies of science, but also from such unexpected sources as chemical and labor journals, reports of the Smithsonian Institution, the Incorporated Association of Architects and Surveyors (London), and Kyushu Imperial University. Argentine, Australian, East and South African, German, Italian, Mauritian, New Zealand, and Swedish publications are included, in addition to the British and Japanese.

Listed also are at least 77 unpublished theses from seven forestry schools; these include Samuel N. Spring's of 1902 and Ferdinand A. Silcox's of 1904 from Yale.

The earliest article noticed is Buckley's of 1860 on "The cutting ants of Texas"; one of these insects still, as the appendix mentions, "precludes pine regeneration, natural or planted, in spots up to 10 acres in size around their large colonies." The cutoff date for citations in the bibliography is June 1959, less than 16 months before the book came off the press.

To have found, retrieved, and abstracted this vast number of publications and reports is a rare feat of scholarship. To have enriched the results of the work so greatly by evaluating and knitting together the scattered facts into a sound and useful whole is a professional accomplishment of the highest order.

Minor criticisms are possible, of course. The tree in the frontis-piece, for example, has not been progeny-tested, and should therefore be described as "plus" rather than as "elite." Some typographical errors appear, including the omission of "Mo." in the first citation on page 531, and the transposition of the addresses of the first and third listed sponsors of the volume. More seriously, reference to Betts 1909 shows that the tabulated heights above stump on page 456 should be not in inches, but in feet.

One may guess, however, that such flaws arose from meeting the publication deadline. One regrets them, of coure, but in perspective they become as the superficial scratches incurred during the shipment and installation of a massive, finely designed, and beautifully polished monument.

Some Forest Soil Characteristics and Their Relationship to Jack Pine Growth

By
STEVE PAWLUK
H. F. ARNEMAN

INVESTIGATIONS of forest soils and their influences upon tree growth are becoming increasingly important in American forestry. Studies to date in various parts of the country indicate that thorough analyses are required to obtain a proper evaluation of the influence of the edaphic factors upon tree growth. The general occurrence of jack pine (*Pinus banksiana* Lamb.) in the Lake States and the broad distribution in Canada justifies a careful investigation into the relationships existing between this species and the characteristics of the soil upon which it grows. Past and presently active investigations in forest soils have been largely confined to other tree species.

Historical

In establishing forest growth and soil relationships many approaches have been considered, but the majority involve correlation of site index and various soil properties. Among the numerous research workers in this field Perry (1928), Stoeckeler (1960), and Young (1954) considered only the individual soil properties for establishing site-growth relations while Gardner and Lyford (1955), Kittredge (1938), and Turner (1937) treated the numerous soil characteristics as independent variables and established site quality classes on the basis of the soil as a whole. In some cases these characteristics were expressed in terms of soil type and phase. Soil characteristics selected for evaluation of site quality are extremely variable. The importance of soil physical properties for tree growth has been stressed by Auten (1940), Locke (1941), and Plair (1952) in their investigations; Forrestall and Gessel (1955) and Youngberg and Scholz (1949) placed a great deal of emphasis on the importance of chemical properties. Results appear to vary with the region and the tree species considered.

Recently major stress has been placed on soil series, type, and phase and their use as a guide for forest growth predictions (Gardner and Lyford 1955). This approach considers all, rather than any one individual characteristic of the soil. In this study emphasis was placed on soils in order to provide an approach to site-index evaluation in terms of a variety of soil site-index correlations based on individual features and detailed profile characteristics.

Experimental

Eighteen 1/10-acre jack pine plots were selected for the study, 16 in north central Minnesota and the other two a short distance south of Port Edwards, Wisconsin. In view of the large number of factors which could influence tree growth, it was decided to equalize external drainage, stand density, slope aspect, and slope range, as much as possible to eliminate possible in-

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teractions with soil profile variations. The study was limited to sites with good external drainage and with undulating to gently undulating topography. Stand age was kept as close as possible to 50 years. The stands were composed of well stocked, relatively pure, even-aged jack pine of similar past history. Under these conditions growth differences were confined closely to variations in soil characteristics. Genetic variations between the jack pine stands at the various sites no doubt exist.

The average frost-free period for the study area varies from 110 to 120 days. The average summer precipitation ranges between 16 and 22 inches and the annual precipitation between 22 and 32 inches. The average July temperature varies from 68 to 70°F.

Site indices were determined for each plot according to the procedure followed by the U. S. Department of Agriculture, Lake States Forest Experiment Station. Site indices were determined, using three dominant and two codominant trees nearest the center of the plot; their values are shown in Table 1.

Soil profiles were exposed by digging pits to a depth of 48 inches approximately in the center of the plots. Individual soil horizons were sampled in each pit. The lower horizons were sampled with a bucket auger. Samples of surface organic matter included the F and H layers only.

All samples were passed through a 2mm sieve prior to analyses. Particle size was determined by the standard U.S.D.A. procedure for pipette analyses and moisture content at 0.1 and 15 atmospheres by using a porous plate and pressure membrane (U. S. Salinity Lab. 1954). The difference between the two values was used as a measure of aivailable moisture holding capacity. Bulk density was measured on core samples taken with a steel cylinder which was carefully driven into the soil. Exchangeable cations were extracted by a method outlined by Bentley and Rost (1947). Total cation exchange capacity was determined both by summation and by the magnesium oxide method (AOAC 1950). The ammonium acetate leachate was prepared for the determination of exchangeable metallic cations according to Fields *et al.* (1951). Exchangeable potassium was determined with a Perkin-Elmer flame photometer using a propane flame and exchangeable calcium and magnesium by a modification of the Cheng and Bray (1951) procedure as outlined by Pawluk[1]. A procedure outlined by Russell and Stanford (1954) was followed for exchangeable hydrogen analyses. The soil paste method (Doughty 1941) was used for pH determinations. Available phosphorus was measured both in extracts with Bray's No. 1 solution and Morgan's reagent (Morgan 1941). The Kjeldahl-Welforth-Gunning method was followed in total nitrogen determinations and the dry combustion method for organic carbon (AOAC 1950). A staining technique was used for light mineral determination (Reeder and McAllister 1957). Standard petrographic procedures were followed for the identification of the heavy minerals. Fine and very fine sand fractions were used for the mineralogical study.

Most of the data were subjected to statistical analyses in order to test the reliability of the relationships which appear to exist between site index and some of the soil properties. The data presented in Table 2 are based on linear regressions. Curvilinear regressions were also calculated for the properties which have a profound influence upon the moisture regime and fertility of the soils. These data are illustrated in Figures 1, 2, 3 and 4. Correlations for the curvilinear regessions are based on 16 degrees of freedom where $r = .468$ and $.590$ for 5 percent and 1 percent of significance, respectively.

[1]Exchangeable cation characteristics of some west central Alberta soils. Unpubl. M.S. thesis, Univ. of Alberta, Edmonton, Canada. 1955.

TABLE 1. Some features observable in the field and their relations to site index.

Soil type	Field site	Site index	Very fine sand + silt + clay (A_2 horizon, %)	Characteristics of the B horizons	Parent materials
Faunce L.F.S.	1	71	29.2	Friable color B	Well sorted outwash sand from the gray drift
Onamia S.L.	2	71	29.7	Cemented iron B	Poorly sorted outwash gravel from the gray drift
Rockwood L.F.S.	3	71	26.2	Cemented iron and textural B	Gray glacial till
Chetek S.L.	4	69	36.6	Cemented iron B	Poorly sorted outwash from the red drift
Onamia L.F.S.	5	67	27.8	Cemented iron B	Poorly sorted outwash from the gray drift
Todd L.S.	6	65	25.1	Cemented iron B	Poorly sorted outwash gravels from the gray drift
Todd F.S.L.	7	64	42.8	Cemented iron B	
Unnamed F.S.L.	8	62	48.9	Firm blocky textural B	Gray glacial till
Menahga L.F.S.	9	61	26.7	Loose color B	Well sorted outwash sands from the gray drift, clay bands in the parent material
Omega L.F.S.	10	59	22.4	Loose color B	Well sorted outwash sand from the red drift
Menahga L.F.S.	11	56	15.4	Loose color B	Sorted outwash sands from the gray drift
Menahga S.	12	55	10.0	Loose color B	Sorted outwash sand from the gray drift with clay bands in the parent material
Omega L.F.S.	13	50	16.6	Loose color B	Well sorted outwash from the red drift
Faunce S.	14	50	13.2	Loose color B	Well sorted outwash from the gray drift
Menahga L.Co.S.	15	49	17.0	Loose color B	Well sorted outwash sand from the gray drift
Menahga F.S.	16	46	8.0	Loose color B	Outwash sand from the gray drift reworked by wind
Plainfield F.S.	17	44	10.0	Loose color B	Outwash sand well sorted by the Wisconsin River
Plainfield F.S.	18	38	9.0	Loose color B	Outwash sand well sorted by the Wisconsin River

Soil Series Characteristics

Profile descriptions. The soils included in this study represent eight soil series; namely Menahga, Omega, Faunce, Plainfield, Onamia, Chetek, Todd, Rockwood, and an unnamed double profile.

The Menahga, Omega, Faunce, and Plainfield soil series developed on well

TABLE 2. Linear correlations betweensite index and soil characteristics.

Soil characteristics	Soil horizons					
	A_{00} & Ao	A_2	B_2	$A_2 + B_2$	$A_2 + B_2 +$	A_{00} & Ao $A_2 + B_2$
Mechanical fractions						
(i) Clay		.353	.523*			
(ii) Silt + clay		.724**	.783**			
(iii) Very fine sand + silt + clay		.590**	.804**	.806**	.794**	
(iv) Very fine sand + silt		.722**	.747**			
(v) Fine sand + very fine sand + silt + clay		—.228	.089			
(vi) (Very fine sand + silt + clay) depth		.583*	.616**	.702**		
Available moisture holding capacity	.440	.633**	.608**	.572**	.582*	
Bulk density			.397			
Total nitrogen content	.038	—.525*	.426			
Total carbon		—.484*				
C/N ratio	—.158	.099	.075			
Available Phosphate						
(i) Extracted with Bray's No. 1 solution	.038	.472*	—.229			
(ii) Extracted with Morgan's reagent	.330	.135	.139			
Exchangeable Cations						
(i) Total exchange capacity		.234	.537*	.489*	.595**	
(ii) Exchangeable potassium	.024	.419	.521*		.595**	
(iii) Exchangeable calcium + magnesium	.439	.320	.495*		.527*	
(iv) Exchange acidity	—.198	.419	.175	.268		
(v) % base saturation	.548*	.438	.445	.256		.580**

*Significant at 5 percent level. **Significant at 1 percent level.

sorted sands. The Menahga, Omega, and Plainfield soil series show similar morphological characteristics. The surface organic material is primarily a *mor* layer. The loamy fine sand to sand A_2 horizons are variable in depth, often present only

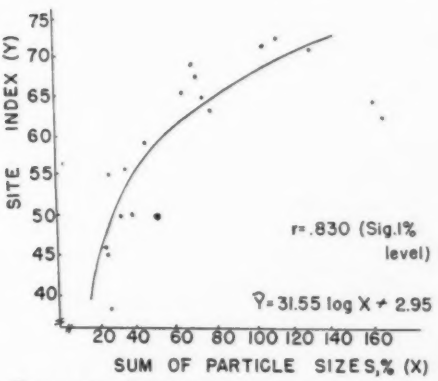

FIGURE 1. *Relationship between site index at age 50 years and the sum of the very fine sand, silt, and clay content of the A_2 and B horizons.*

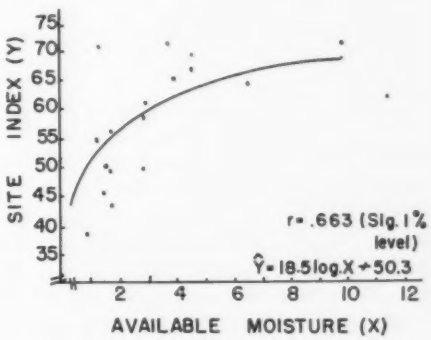

FIGURE 2. *Relationship between the sum of the available moisture holding capacity (inches) in the A_{00}, A_2, B_2, and B_3 horizons and site index at age 50 years.*

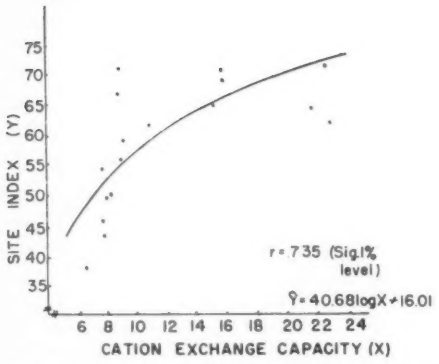

FIGURE 3. *Relationship between site index at age 50 years and the sum of the cation exchange capacities in Milliequivalents per 100 grams of soil of the A_2 and B horizons.*

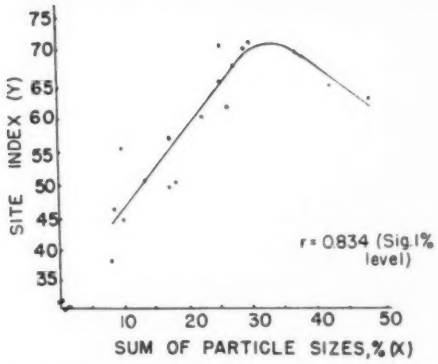

FIGURE 4. *Relationship between the sum of the very fine sand, silt, and clay content of the A_2 horizon and site index at age 50 years.*

as incipient horizons but may attain depths from four to six inches. The low base status, lack of clay movement, moderate degree of weathering along with morphological features place these soils in the Brown Podzolic great soil group. In local areas the morphological features tend toward podzols.

The Onamia and Chetek soil series are characterized by eluviated A_2 horizons, cemented B horizons and outwash gravel C or D horizons. The base status of the upper sola and the percentage base saturation throughout the sola are fairly high. These soils appear to be Gray Brown Podzolic-Podzol intergrades.

The Rockwood and Todd soil series have a high base status and a textural B horizon. The Rockwood soil series is developed from limy till and the Todd soil series from limy outwash material. These soils are classified as Gray Wooded.

A double soil profile included in this study shows polygenetic development with a podzol developed in the A_2 horizon of the original till profile. The soil may be classified as a Podzol-Gray Wooded intergrade but the series is unnamed.

Mechanical composition. Variations in mechanical analyses, as shown in Table 3, reflect different degrees of geological sorting and morphological development. The Menahga, Omega, Faunce, and Plainfield soil series have uniform, well sorted, sandy parent materials. The clay content in the A horizons is greater or equal to the clay content of the B horizons, indicating a lack of eluviation.

The Onamia, Chetek, and Todd soil series are developed on poorly sorted outwash material. The parent materials are heterogenous, with the coarse sands and gravels of the unaltered parent materials overlain by finer deposits which contain considerable amounts of silt and clay.

The Rockwood soil series and the unnamed soil with a double profile are developed on unsorted glacial till. The B_2 and B_3 horizons of both series show a marked illuviation of clays. The podzol-like B horizon of the double profile soil shows little or no evidence of clay accumulation from the podzol A_2 horizon.

Available moisture holding capacity. The moisture regime of the soils (Table 3) is influenced by such factors as an increase in organic matter content and the amount of fine materials. Either or both of these factors improves the water holding capacity of the soil.

TABLE 3. Summary of the physical properties of the soils by series.

Series, horizons, and depths	Mechanical composition						Available moisture holding capacity (0.1 atm-15 atm) (Percent by weight)	Available moisture holding capacity (Inches)
	Gravel (Percent of total soil)	Very coarse, coarse, and medium sand	Fine sand	Very fine sand	Silt	Clay		
	(Percent based on fraction less than 2 mm)							
Faunce								
Aoo & Ao 1-10″	—	—	—	—	—	—	20.7	.16
A_2 0-1″	0	43.1	30.3	6.2	12.8	2.3	6.3	.07
B_2 1-10″	3	50.8	28.3	5.5	13.2	2.4	6.0	.78
B_3 10-19″	5	43.5	36.7	8.3	10.4	1.7	4.6	.54
C_1 19-39″	2	60.9	27.5	4.0	7.0	0.7	3.0	.08
C_2 39-60″	5	79.3	19.2	1.5	0.8	0.1	0.6	.15
Onamia								
Aoo & Ao 2-0″	—	—	—	—	—	—	11.8	.19
A_2 0-4″	8	51.1	20.3	7.6	15.1	4.2	7.3	.41
B_2 4-12″	11	63.7	16.4	5.9	22.8	4.6	9.9	1.11
B_3 12-23″	5	49.1	18.0	9.2	21.5	6.9	8.4	1.35
C_1 23-38″	19	56.5	29.6	6.8	7.6	2.7	4.2	.90
C_2 38-51″	21	73.1	14.3	3.1	7.6	2.3	4.6	.79
Rockwood								
Aoo & Ao 1.5-0″	—	—	—	—	—	—	19.2	0.12
A_2 0-12″	2	33.6	40.2	9.1	15.0	2.1	6.7	1.21
B_2 12-18″	5	19.9	30.6	9.5	29.0	11.0	9.8	0.74
B_3 18-20″	5	24.2	19.9	8.5	28.4	19.0	14.7	0.11
C_1 20-42″	5	19.3	23.4	12.3	32.5	12.5	14.6	4.20
C_2 42-60″	5	23.2	23.4	8.2	35.4	9.8	14.2	3.21
Chetek								
Aoo & Ao 2-0″	—	—	—	—	—	—	15.8	0.25
A_2 0-3″	0	41.6	21.5	2.2	29.4	5.0	10.6	0.46
B_2 3-16″	21	55.3	14.4	3.5	23.9	2.9	7.5	1.41
B_3 16-24″	55	74.7	16.2	2.5	1.9	4.7	3.3	0.38
C_1 24-42″	26	55.5	16.1	3.1	23.6	0.9	9.0	2.24
C_2 42-60″	15	78.1	18.0	1.2	2.7	0.0	1.4	0.36
Todd								
Aoo & Ao 2-0″	—	—	—	—	—	—	16.2	0.26
A_2 0-19″	8	39.4	26.6	5.9	22.7	5.8	9.4	2.55
B_2 19-26″	28	53.5	19.2	3.3	11.2	10.3	13.8	1.89
B_3 26-30″	34	74.9	11.3	1.5	6.7	5.1	6.1	1.30
C_1 30-38″	42	65.7	24.0	1.8	6.7	2.1	4.0	0.48
C_2 38-55″	46	79.5	14.0	1.6	4.2	0.8	3.5	0.36
Unnamed (double profile)								
Aoo & Ao 2-0″	—	—	—	—	—	—	29.2	0.47
A_{2p} 0-3″	9	24.1	29.0	11.8	33.4	3.7	13.5	0.63
B_p 3-13″	5	30.9	27.7	8.8	29.3	3.3	16.9	2.61
A_2 13-18″	5	26.3	22.9	10.1	34.9	6.3	10.8	0.83
B_2 18-26″	6	25.9	18.3	5.6	30.3	19.9	12.6	1.56
B_3 26-36″	4	23.2	18.2	10.0	33.3	15.3	13.9	2.15
C_1 36-48″	4	18.1	23.4	9.0	34.7	14.8	14.9	2.77
C_2 48-60″	9	23.9	21.0	8.7	33.9	11.5	13.8	2.57
Menahga								
Aoo & Ao 1-0″	—	—	—	—	—	—	14.3	0.11
A_2 0-4″	1	40.8	45.7	4.7	7.4	3.3	2.7	0.15
B_2 4-12″	1	47.4	42.7	5.0	12.7	3.0	4.0	0.44
B_3 12-22″	4	45.1	42.5	6.2	3.9	2.3	3.3	0.42
C_1 39-63″	1	57.9	38.0	2.4	1.1	0.6	1.1	0.21

TABLE 3. (Continued)

Series, horizons, and depths	Mechanical composition						Available moisture holding capacity (0.1 atm-15 atm) (Percent by weight	Available moisture holding capacity (Inches)
	Gravel (Percent of total soil)	Very coarse, coarse, and medium sand	Fine sand	Very fine sand	Silt	Clay		
	Percent based on fraction less than 2 mm)							
Omega								
Aoo & Ao 2-0″	1	.....	.....	.....	.....	.....	14.6	0.23
A_2 0-4″	1	28.0	51.7	2.3	13.8	3.5	8.5	0.51
B_2 4-16″	0	46.7	39.6	3.2	9.1	2.4	5.6	1.06
B_3 16-35″	0	32.9	55.3	5.3	5.2	1.4	3.4	0.84
C_1 35-43″	0	68.9	28.4	1.4	0.3	0.6	1.2	0.12
C_2 43-65″	0	39.7	53.7	4.9	1.2	0.6	1.7	0.49
Plainfield								
Aoo & Ao 2-0″	0	.....	.....	.....	.....	.....	9.4	0.15
A_2 0-3″	0	36.7	53.9	3.0	4.6	2.0	3.2	0.14
B_2 3-14″	0	48.3	42.3	4.0	4.3	1.9	3.0	0.48
B_3 14-35″	0	39.9	53.4	4.7	1.9	0.2	1.3	0.19
C_1 35-51″	0	57.5	40.2	1.5	0.7	0.2	1.6	0.36
C_2 51-70″	0	46.0	47.9	5.1	1.0	0.0	0.4	0.09

Available phosphorus. Phosphate studies[2] have established a close relationship between aluminum phosphate content in soils and phosphate extracted by Bray's No. 1 solution. Calcium phosphates and a portion of the iron phosphates are also removed by the acids used in this extracting solution. It has also been established that results from Morgan's method of extraction are closely related to the more soluble calcium phosphates and the adsorbed phosphates in the soils. Available phosphate as determined by Morgan's and Bray's No. 1 reagents is shown in Table 4. The low amounts of calcium phosphates, as determined by Morgan's reagent, indicate that the phosphates of the upper mineral horizons are primarily aluminum and iron phosphates. This is especially obvious in the color B horizons and the podzol B horizon of the double profile soil, while the forest floor, on the other hand, shows higher concentrations of calcium and adsorbed phosphates. These results indicate that the combined phosphorus varies considerably in the various horizons of the sola, both in quantity and form.

Organic carbon. Organic carbon × 1.73 indicates organic matter content in the soils. The upper soil sola appear to vary in the amount of organic matter present.

Carbon-nitrogen ratio. All soil horizons included in this study show a continual decrease in C/N ratio with progression in depth (Table 4). Apparently organic mattera can move mechanically down the sola prior to complete decomposition. This is especially obvious in the coarser textured profiles. Active decomposition or selective movement of the organic matter is evident in both the A_2 and B horizons.

Soil reaction and cation exchange properties. The data for soil reaction and exchange properties are shown in Table 4. Total cation exchange capacities for the Faunce, Menahga, Omega, and Plainfield soil series reflect a large degree of immaturity in soil profile development. Total cation exchange capacities are highest at the surface and progressively decrease down the sola. There is evidence of a

[2]Cho, C. M. Available phosphorus and forms of phosphorus in several soils of Minnesota. M.S. Thesis. Univ. of Minnesota, St. Paul, Minn. 1957.

TABLE 4. Summary of the chemical properties of the soils by series.

Soil series and horizons	pH	Available phosphorus (ppm) Morgan's	Bray's No. 1	Organic Nitrogen (percent)	carbon (percent)	C/N ratio	Exchangeable cations (me/100 gm) Ca	Mg	K	H	C.E.C. (me/100 gm by sum)	Base (Saturation percent)
Faunce												
Aoo & Ao	4.4	23.0	35.3	0.838	27.83	35	19.8	3.0	1.39	33.6	57.8	42
A_2	4.7	0.8	27.9	0.036	0.94	26	0.9	0.2	0.08	2.1	3.3	37
B_2	5.6	1.8	67.7	0.020	0.33	16	1.3	0.2	0.09	1.2	2.8	56
B_3	5.7	1.8	33.5	.....	.....	...	0.8	0.2	0.04	0.6	1.6	72
C_1	5.8	0.3	28.4	.....	.....	...	0.6	0.2	0.02	0.2	1.0	88
C_2	6.0	0.0	7.8	.....	.....	...	0.7	0.2	0.03	0.0	0.9	100
Onamia												
Aoo & Ao	5.2	13.3	29.3	0.289	8.00	29	10.5	1.6	0.48	6.1	18.7	66
A_2	5.0	3.0	56.7	0.031	0.57	19	1.5	0.3	0.14	1.9	3.8	53
B_2	5.4	3.5	47.9	0.021	0.25	12	2.1	0.4	0.15	0.9	3.6	73
B_3	5.7	3.0	29.9	.....	.....	...	2.8	0.6	0.09	0.6	4.1	80
C_1	5.9	1.0	16.7	.....	.....	...	1.9	0.3	0.09	0.2	2.5	91
C_2	5.9	0.5	11.4	.....	.....	...	1.8	0.4	0.06	0.2	2.5	92
Rockwood												
Aoo & Ao	6.4	14.0	24.1	0.612	16.87	28	19.8	7.8	0.94	2.5	30.2	92
A_2	5.8	2.5	70.0	0.016	0.27	17	1.3	0.3	0.09	0.4	2.1	81
B_2	5.4	1.0	18.3	0.024	0.25	10	4.8	1.5	0.20	0.7	7.2	90
B_3	6.6	1.0	4.9	.....	.....	...	9.4	3.4	0.19	0.1	13.1	99
C_1	7.3	0.5	3.4	.....	.....	...	15.7	1.0	0.14	0.0	16.8	100
C_2	7.8	0.5	2.3	.....	.....	...	16.1	1.1	0.10	0.0	17.3	100
Chetek												
Aoo	4.8	17.5	35.1	0.473	14.70	31	15.4	1.6	0.92	12.7	30.6	58
A_2	5.6	5.0	64.8	0.053	0.91	17	5.4	0.7	0.18	1.5	6.4	17
B_2	5.7	6.5	117.5	0.043	0.53	12	2.5	0.3	0.16	2.2	5.2	58
B_3	5.9	2.5	114.0	.....	.....	...	1.9	0.3	0.16	0.7	3.1	77
C_1	6.1	0.0	13.0	.....	.....	...	1.8	0.4	0.09	0.8	3.1	74
C_2	5.8	0.0	3.8	.....	.....	...	1.7	0.5	0.08	0.1	2.4	96
Todd												
Aoo & Ao	5.1	4.0	12.3	0.427	7.79	19	13.6	2.0	0.60	6.6	22.8	72
A_2	5.3	1.8	44.8	0.024	0.30	11	2.5	0.6	0.12	1.3	4.5	76
B_2	5.7	2.3	31.5	0.022	0.20	9	6.4	1.8	0.15	1.0	9.4	89
B_3	6.7	1.0	12.3	.....	.....	...	3.9	2.0	0.08	0.1	6.1	96
C_1	6.8	1.0	11.8	.....	.....	...	4.5	0.8	0.05	0.1	5.5	94
C_2	7.1	0.5	7.9	.....	.....	...	3.0	0.5	0.04	0.0	3.5	100
Unnamed	(double profile)											
Aoo & Ao	5.2	21.0	31.4	0.497	19.05	38	20.8	3.6	0.90	11.9	37.2	68
A_{2p}[1]	5.9	1.0	21.3	0.042	1.15	27	3.3	0.5	0.08	0.6	4.5	87
B_{pu}	5.9	2.0	111.3	0.066	1.20	18	3.3	0.6	0.25	2.5	6.7	63
A_2	5.3	0.5	4.4	0.009	0.12	13	1.3	0.6	0.33	0.6	2.5	76
B_2	4.8	1.0	7.2	0.016	0.16	10	6.2	3.5	0.16	1.9	11.8	84
B_3	5.2	0.0	3.1	.....	.....	...	6.3	3.8	0.12	0.9	11.1	92
C_1	5.6	0.0	3.4	.....	.....	...	7.7	1.3	0.12	0.6	9.7	94
C_2	6.3	0.0	3.6	.....	.....	...	7.8	1.2	0.11	0.2	9.3	98
Menahga												
Aoo & Ao	4.8	15.5	20.8	0.663	21.19	33	13.4	2.6	1.01	11.1	28.1	54
A_2	5.6	1.5	42.9	0.037	0.80	19	2.4	0.4	0.11	1.0	3.9	70
B_2	5.7	1.6	68.8	0.017	0.23	13	1.4	0.5	0.09	0.5	2.5	72
B_3	5.7	1.4	56.0	.....	.....	...	1.1	0.2	0.07	0.3	1.7	81
C_1	6.0	0.5	15.9	.....	.....	...	0.9	0.2	0.08	0.1	1.3	88
C_2	6.2	0.3	8.3	.....	.....	...	1.1	0.2	0.05	0.1	1.5	96

TABLE 4. (Continued)

Soil series and horizons	pH	Available phosphorus (ppm) Morgan's	Bray's No. 1	Nitrogen (percent)	Organic carbon (percent)	C/N ratio	Exchangeable cations (me/100 gm) Ca	Mg	K	H	C.E.C. (me/100 gm by sum)	Base (Saturation percent)
Omega												
Aoo & Ao	4.6	5.8	11.3	0.421	10.36	25	12.6	1.4	0.71	7.7	22.4	61
A_2	4.8	1.3	33.7	0.043	0.86	20	1.1	0.2	0.11	2.3	3.7	34
B_2	5.2	1.5	63.3	0.023	0.21	9	0.9	0.2	0.15	1.3	2.6	53
B_3	5.5	1.2	32.8	.....	.....	....	0.9	0.2	0.10	0.7	1.9	80
C_1	5.9	0.0	18.3	.....	.....	....	0.8	0.1	0.06	0.1	1.1	94
C_2	5.9	0.0	6.4	.....	.....	....	0.9	0.2	0.07	0.0	1.2	100
Plainfield												
Aoo & Ao	4.8	9.0	25.2	0.400	15.81	42	7.7	0.8	0.42	11.2	20.1	45
A_2	4.8	2.0	15.9	0.062	1.48	24	1.3	0.1	0.09	3.0	4.5	30
B_2	5.3	0.0	63.5	0.026	0.32	12	0.4	0.1	0.06	1.0	1.6	39
B_3	5.7	0.0	40.7	.....	.....	....	0.2	0.1	0.04	0.4	0.7	41
C_1	5.7	0.0	31.0	.....	.....	....	0.2	0.0	0.05	0.1	0.4	75
C_2	5.8	0.0	18.5	.....	.....	....	0.1	0.0	0.03	0.0	0.1	0

[1]Podzolized horizons.

minimum of eluviation of colloids from the A_2 horizon since exchange capacity reflects colloid content; this is corroborated by the results obtained from mechanical analyses. The colloidal content is low for all mineral horizons. The sola have their lowest degree of base saturation in the A_2 horizons while reaction is lowest at the surface and progressively increases with depth.

In the Onamia, Chetek, and Todd soil series, exchange capacities are higher in the sola than in the parent materials and reflect the heterogeneity of the parent materials. Base saturation of the Onamia and Chetek soil series is low in the upper part of the solum. The Todd soil series, on the other hand, has a higher degree of base saturation. The higher exchange capacity by summation as compared to the exchange capacity by determination and the pH indicate the presence of lime in the parent materials of these soil series.

In the Rockwood soil series, the presence of high quantities of exchangeable calcium, high exchange capacity found by summation as compared to the exchange capacity by determination, and the alkaline reaction reflect the presence of lime in the parent material. The pH is lowest in the B_2 horizon.

The double-profile soil included in this study has its highest total cation exchange capacity in the B horizon of the original profile and in the Bp of the miniature profile. The pH attains a minimum in the B_2 horizon.

Correlations Between Site Index and Soil Properties

Physical properties. The highly significant correlation between site index and physical properties are shown in Table 2, and Figures 1, 2, and 4. The data presented in Table 2 are based on linear regression analyses while the curves in Figures 1, 2, and 4 are calculated from equations established by curvilinear regression analyses. The *r* values are only slightly higher for curvilinear regressions than for linear regression for the same data and are not significantly different as demonstrated by an analysis of variance (*f*-test).

Highly significant relationships between jack pine growth and the content of very fine sand, silt and clay in the upper portions of the soil sola were found to occur.

It is evident that available moisture holding capacity is one of the most important

factors in tree growth. This relationship, as illustrated in Figure 2, suggests a rapid increase in site index with an increase in water holding capacities up to a certain point after which there is little effect on site with further increases in moisture holding capacity. Horizon depth and physical properties of soils with reference to site index show significant relationships but lower correlations are obtained when the entire solum is considered. The depth factor was applied as an interaction with the physical factors only because the functional relationship between horizon depth and tree growth had not been established for the soil considered in this study. This functional relationship depends upon the genetic and inherent features of the soil profiles as well as the surface area of the roots in contact with the soil, e.g. tree growth could not be expected to show twice the response to a horizon 4 inches deep when compared to a horizon 2 inches deep. Horizon depth alone is better correlated with site in those regions that have tree roots restricted by impenetrable soil horizons or impermeable geological substrata (Coile 1935).

Chemical properties. Correlations between carbon-nitrogen ratios of the soils and site index are non-significant (Table 2). The total nitrogen and carbon contents in the A_2 horizon of all soils show significant negative correlations with site index. From these results it may be concluded that a negative correlation exists between organic matter of the A_2 horizon and site index. Correlations between total nitrogen in the B horizon and site index are below the 5 percent level of significance.

Carbon-nitrogen ratios may be considered as a measure of active decomposition of organic matter. The consistently high ratios in the entire solum indicate that nitrogen release is probably very slow and that extreme competition exists between the soil microorganisms and plant roots for available nitrogen. Since microorganisms are considered to assimilate available nitrogen without release above a carbon-nitrogen ratio of 10 to 1 (Waksman and Starkey 1949), the lack of available nitrogen may be a factor in site growth potential.

Available phosphorus in the A_2 horizon, as determined by Bray's No. 1 solution, correlates significantly with site index but available phosphate in the A_{oo}, A_o and B_2 horizons shows no correlation, even though there are larger quantities present in these horizons. A considerable amount of the available phosphorus in the B horizons of these soils, as determined by Bray's No. 1 solution, may be in a form which is not available to the tree roots. Available phosphorus, as determined by Morgan's reagent, shows no significant correlation for any soil horizon with site index (Table 2). A lack of knowledge concerning the uptake of phosphorus by jack pine roots does not permit any definite conclusions to be drawn at this time.

Correlations of site index and the ion exchange properties of the soil are shown in Table 3. Total cation exchange capacity of the solum is shown to be significantly related to site index (Figure 3). However, when the forest floor is included with the solum the relationship no longer holds true. The forest floor was thin at all sites and had a fairly high total exchange capacity. The upper layer of forest floor was loose and dry with the roots concentrated in the lower 0.25 to 0.50 inches. The exchangeable metallic cations (calcium, magnesium and potassium), correlated significantly with site index; these correlations are most obvious when the entire soil solum is considered. The exchange acidity of the soil showed no significant correlations with site index. The percentage base saturation showed a significant decrease with a reduction in site index. It has been shown that decreases in base saturation reflect decreases in soil fertility; therefore, it would obviously affect the growth potential of the site.

Relation of Soil Features to Site Index

Table 1 summarizes some of the more important morphological features which are

readily observable in the field, and their relation to site index. On the basis of the data presented it may be concluded that upland soils developed on outwash sands, without any restricting layers and having loose B horizons, range in site index from 38 to 59. The most obvious relation exists between site index and quantity of very fine sand, silt, and clay in the surface horizons (Figure 4). Sites 9 and 12 are similar to the group without restricting layers and loose B horizons, but thin clay bands interbedded in the substrata increase their site quality. This is to be expected since the bands provide a restriction to percolation and increase the amount and the electrolyte status of ground water. These soils are differentiated from soils lacking restricting layers through the use of soil phase separations.

The major group of sites included in the site index range from 38 to 59 may be separated on the basis of soil type. The surface soils which have a fine sand texture have a site index below 50. This group of soils has a clay content that is very low, therefore, the nutrient status is expected to be more closely related to the mineralogy of the sands. The Plainfield sands are found in areas of higher precipitation and more favorable growth conditions, than the other soils in the lowest site quality range. The poor growth of jack pine in this region can at least be partially accounted for by the deficiency of base-rich minerals. The outwash sands from the red and gray drifts in Minnesota are fairly rich in nutrient-supplying minerals, and therefore, do not warrant separation from each other for assessing jack pine site quality.

The morphologically similar profiles of Menahga, Omega, and Faunce soil series have similar growth potentials for jack pine provided their surface textures are similar. The increase in fineness of texture in the surface horizon and the change from a loose to a more friable consistency is readily discernible in the field.

The second major group of sites in Table 1 which range in site index from 62 to 71 are characterized by B horizons with pronounced structure. A first subdivision of this group is exemplified by the soil in site 1. The soil differs from the previously discussed soils in that the finer textured material extends to greater depths in the solum, in this instance, to the bottom of the B_3 horizon. The increase in finer textured material results in the formation of a B horizon with a friable, rather than loose consistence which is easily recognized in the field. The soil in this case is immature and further leaching could possibly result in the formation of a cemented or indurated B horizon. A second subdivision of the group is comprised of those soils which have cemented or textural B horizons; these horizons are impenetrable when dry but are less cemented when wet. This group includes the Onamia, Todd, Chetek, and Rockwood soil series, as well as the unnamed soil. The B horizons of these soils may restrict root development but have a beneficial value in reducing the loss of water by percolation.

Variations in the substrata under strongly developed B horizons appear to have little effect upon site quality. Very few differences can be observed among the sites with a substrata composed of sorted outwash sands, outwash gravels, or glacial till, despite the variation in particle size distribution. Variations in site indices for such regions are primarily the functions of the soil characteristics above the restricted B horizon. Because the A_2 horizons have similar depths in those profiles with strongly developed B horizons, it is difficult to evaluate their influences upon growth in the present study. It is interesting to note that sites 4, 7 and 8 have lower site indices and higher fractions of very fine sand, silt, and clay. On the basis of the data presented, it appears that increases in the sum of the three fine fractions beyond 30 percent of the total, has a depressive effect on growth when underlain by impermeable horizons (Fig. 4). The decrease in aeration of a soil in conjunction with an in-

crease in the content of the finer soil separates may explain the depressive effect upon growth.

Conclusions

It may be concluded from the limited data presented in this study that growth of jack pine in the region concerned is closely related to those characteristics of the soil which influence both fertility and available moisture holding capacity. Therefore, to obtain a reliable evaluation of site quality, the logical approach would be to integrate these characteristics and consider them as a whole. Mechanical composition is the best direct measure of both moisture holding capacity and cation exchange capacity. Silt and clay content of the soil correlate closely with moisture holding capacity. Colloidal clay, in the presence of low quantities of organic matter, makes up a major portion of the cation exchange complex. The entire solum presents a better estimate of growth potential than does any one horizon. When using laboratory analyses as the basis for evaluating growth potential for jack pine, the morphology of the soil solum should be included since the importance of many characteristics is also influenced by the morphological constitution of the profiles.

Land use mapping units for the soils discussed in this study may be set up as arranged in Table 1. However, since soil type provides an excellent description of all morphological characteristics, it may, be better to map the soils on the basis of soil type and later group them for growth potential. Stoeckeler (1960) from his aspen studies in the same region of Minnesota, concluded that site indexes were related to parent materials. His gravel areas had much lower site indexes than areas of glacial till but this was not the case with jack pine sites. The use of mapping units based on soil properties shown in Table 1 would be suitable for jack pine but would require different groupings for aspen. A soil type map would provide details of soil characteristics with sufficient information of a nature suitable for evaluating site quality for both species. Soil type maps, should therefore, be very helpful in evaluating growth potential in regions of diversified soils provided that the grouping of soil types having similar potential is based upon careful laboratory and field studies which show the relation between the individual soil characteristic and growth of the trees.

Summary of Results

1. Significant correlations were found to exist between soil physical and, to a lesser extent, chemical properties and site index for jack pine.
2. Soil properties which have a profound influence upon the moisture regime and fertility show highly significant curvilinear correlations with the growth of jack pine.
3. A definite relationship appears to exist between the morphological features of the soil and jack pine growth; together with laboratory analyses the limited data indicate that this could be used as a suitable approach for site evaluation.
4. Although physical and chemical properties correlate significantly with site index, it is difficult to state any one factor which might be most limiting to jack pine growth.
5. Soil type maps express all the morphological features and parent materials of soils with a reasonable amount of detail. Accompanied by laboratory analyses these features should provide suitable criteria for evaluating site provided the various soil types are regrouped in accordance with the properties that are closely related to the growth of jack pine. The soil type maps may also prove to be useful for other species providing a regrouping of soils is conducted on the bases of field and laboratory studies for the species in question.
6. The Menahga, Omega, Faunce and Plainfield series are morphologically and chemically similar to Brown Podzolics. Integrades towards podzols

occur in association with the Brown Podzolic Soils.

7. Onamia and Chetek soils have properties characteristically related to Podzols.
8. Rockwood and Todd soil series have characteristics which approach those of the Gray Wooded Group.
9. A bisequa profile found in northern Minnesota consists of a miniature Podzol profile developed in the A_2 horizon of a profile which was formerly either Gray Wooded or Gray Brown Podzolic.

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Foundations of Wildlife Nutrition

Grundlagen der Wildernährung. By Antonin Bubenik. Deutscher Bauerverlag, Berlin, 1959. 299 pp., 25 diagrams, 35 tables. DM 14.20 ($3.50). [In German]

Review by Richard D. Taber
Montana State University, Missoula

Historically, the forests of Europe were the hunting grounds of the aristocracy. Foresters were first a police, responsible for the protection of their masters' game, and often for the control of lawless men lurking in the wood. The demand for greater and greater densities of game led to more intensive management, including winter feeding. The forest was sometimes fenced, to keep the big game animals, especially red deer, from leaving it. The result of high game density maintained by feeding and fencing inevitably was damage to the forest vegetation.

This historical situation is only now beginning to change in central Europe. Game densities are still maintained by artificial feeding, especially in the monotypic forests of planted spruce which make up a large proportion of the timber producing area. Red deer damage to spruce (and many other species) consists largely of barking, and continues in spite of an abundant artificial food supply. Currently, much research is being conducted throughout central Europe, in an attempt to develop ways of alleviating this damage, which is said in West Germany, for example, to reduce the potential production of spruce timber by 10 to 15 percent. Repellants, protective devices and physical modifications of the bark are being tested wholesale.

The author of the volume under review applies new concepts to the solution of this old problem. He is a physiological chemist and vertebrate zoologist who was until 1958 employed in the Research Institute of Forestry and Wildlife Management of the Czechoslovak Academy of Agricultural Science, in Zbraslav. The Institute has its own laboratories and experimental areas, and facilities for working with tamed ruminants. It has as one of its principal aims the integration of wildlife and forest management. The author and his co-workers have taken a broad view of this mission, and have developed a body of basic information on physiology, nutrition, behavior and population dynamics from which scientifically sound recommendations could be derived.

The present volume is written for the sportsman and the land manager, as a review of the current knowledge in the field of nutrition and a guide to supplemental feeding. It embodies a growing appreciation of the need for land managers to understand the natural traits of wild animals and to adapt their methods to them.

The first six pages of the book cover the fundamentals of life processes and the chemical composition of plants and animals. Next comes a more detailed (58 pages) exposition of the nutrients and constituents of the animal body, the nutritional physiology of wild animals, and a consideraion of dietary deficiencies and their effects.

The main portion of the book consists of two parts, one devoted to birds and the other to mammals. Each is introduced with a discussion of individual forms. Under birds, only the partridge, the pheasant, and the dabbling

ducks (as a group) are covered. Under mammals are the hare and rabbit, wild boar, mouflon, chamois, roe deer, red deer, and fallow-deer.

The section on the red deer is among the most comprehensive and the most important for forest management. Therefore, it has been selected for partial review.

The red deer is believed by the author to have been originally a dweller of the open steppe, especially near the fringing forests of lowland streams. In the eastern Carpathians it began to occupy extensive forests only after the canopy had been opened by cutting. Human land use and other interference has forced the red deer to occupy wooded habitat, and to restrict its radius of movement considerably. This restriction has often prevented the upward spring migration to avoid biting insects and also forced the animals to forage over a smaller area, to the detriment of the forest vegetation. This is especially evident in forest plantations, where ground cover is sparse.

Intensive continuous observations, aided by an infra-red viewing apparatus, have resulted in a detailed picture of the seasonal pattern of activity, including foraging and rumination. These studies have led the author to develop his theories of "natural daily rhythm." Disturbances of this rhythm lead to "damage" feeding, such as the bark stripping previously mentioned above. Some disturbance has resulted by the forcing of red deer into a new habitat. Disturbance results if the deer cannot avoid biting insects by moving to new elevations. But the greatest disturbance within the power of management to correct, is the method of winter feeding. The author believes that the present custom of feeding hay and starchy roots, in racks, leads to a serious reduction in the foraging and rumination period, because the food is too unbalanced and too easy to obtain. He recommends first of all the encouragement of natural forest foods, such as blueberry, willow, and heather. Then, artificial feeding is improved in two ways—the quality is improved and, equally important, the difficulty of obtaining the food is increased.

Two methods are recommended for increasing foraging time. One is to place the various dietary components at places removed from one another (chain feeding) so that the individual deer must move from one to another. The other is to prepare, during the summer, a silage of the foliage and small branches of forest trees. This is so tightly compressed that the animals must expend much time in obtaining a sufficient supply. The author believes that by applying these methods, and permitting forest damage in the immediate vicinity of the feeding area (the small area of "winter range" which is selected by the animals themselves) damage to the forest as a whole can be greatly reduced.

Throughout this book, the author has taken a broad approach to the problems of understanding the ecology of wild animals. He is frank in pointing out the many unknowns and imperfectly knowns. While he emphasizes the work of his own institute, he does not ignore others. His bibliography of 121 titles includes 103 from 1950 on, and 24 in English.

The book itself is well printed on the soft paper typical of that used in East Germany, and is well illustrated with graphs and charts. An appendix gives plans for feeding structures.

The reviewer sees in this volume a step away from the highly artificialized wildlife production of central Europe and toward the ecological integration of wildlife management with other land uses.

The Forest Needs Lime

Der Wald Braucht Kalk. Kalkdienst, 1959. Kölner Universitätsverlag, Köln. 239 pages, paper, no price indicated.

Review by Laurence C. Walker
University of Georgia, Athens

This little book is tightly packed with information on woodland liming in Germany. Edaphic and physiologic foundations for liming forests of fir, Scotch pine, beech, poplar, and willow are presented. One of the 30 scientist-forester authors of this symposium of research reports states that the big upswing in liming of German forests came after 1948, when it was clearly recognized that lime stimulates decomposition of raw humus, improves soil structure, encourages growth of soil flora, provides an essential nutrient, and facilitates absorption of other nutrient elements. Liming for the encouragement of natural reproduction of beech was recommended as early as 1902 and was practiced between the World Wars. While not yet economical, it is recommended that certain stands be limed, as well as others fertilized, for production of healthier trees.

Experiments with doses up to 11 tons of CaO per hectare resulted in a significant change in Ca only in the uppermost layer of soil, indicating the strong buffering action of raw humus. Acidity was not reduced sufficiently to be unfavorable to coniferous tree growth, though in some instances it exceeded neutrality.

Soil flora data show that liming increased bacteria, sometimes at the expense of fungi. Nematodes were greatest on areas treated with burned lime and, as expected, earthworms increased greatly after treatment. It is suggested that the improved humus conditions resulting from liming brought about an increase in growth.

Applications of burned lime at rates of 10 to 15 tons per hectare effectively control sphagnum moss where natural reproduction of spruce-fir is desirable and where the brown podzolic soils are covered with a thick mat of raw humus and moss which precludes seedling establishment. The moss turns red and dies, leaving in its wake an odor unpleasant even to wildlife.

In Mg-deficient Scotch pine plantations treated with Mg salts and N-P-K fertilizer for several years, "liming is mandatory for a successful plantation." No concrete reason is suggested. In mixed stands of Scotch pine with beech understory, about ½ pound of lime is placed in the planting hole to increase pH. The higher pH is essential for beech establishment, and the mixed forests are necessary as insects destroy pure stands. In another experiment, height growth of beech was appreciably stimulated (30-60 percent taller) by liming for five years after planting; and good results are suggested if beech sites are limed 2-3 years before planting.

Optimum growth of poplar is obtained on neutral to weakly alkaline soils (pH 6-8 is good; 5-6 is usable). The ash of poplar contains 60-70 percent CaO. Three tons/ha of CaO doubled growth.

Since the fungus causing red heart rot on Scotch pine (possibly *Stereum* sp.) is more prevalent on sites with pH above 5, it is often feared that liming will increase the pathogen's spread. Early experimental results indicate no increase, principally because even limed areas have pH values below 5.

Of entomological interest is the research report that *Lygaeonematus pini* Retz epidemics are discouraged by maintaining soil pH above 6 for several years. The cocoons of this pine sawfly thrive best in soils with pH of about 4.

That the forests of Germany need lime is apparent from the stimulating reports in this paperback volume. While it is assumed that the forests of America are not in this nutritional predicament, a verbatim English translation of *Der Wald Braucht Kalk* is urged. Tree nutrition specialists in this country should be familiar with its contents.

(In this review Klaus Steinbeck, a University of Georgia forestry student, generously gave of his time to help in translation.)

Taxonomic Monograph on the Pines

Les Gymnospermes Actuelles et Fossiles. Chapitre XI. Généralités, Genre Pinus. *By H. Gaussen. Travaux du Laboratoire Forestier de Toulouse, tome II, sect. 1, vol. 1, pt. 2, 272 pp. Illus. Toulouse, France.*

Review by Elbert L. Little, Jr.
Forest Service, U. S. Department of Agriculture

The latest publication from the forestry laboratory at Toulouse, France, contains a taxonomic monograph of the genus *Pinus* for both living and fossil species. This part in the complex numbered series begins with the family Abietaceae and keys to the 10 genera but treats only one genus. Professor Henri Gaussen, of the Faculté de Sciences de Toulouse, has contributed also to earlier parts.

Twenty-three pages are devoted to the principles of classification and evolutionary characters within the genus *Pinus*. The author is skeptical of the value of chemistry, wood anatomy, and hybridization for indicating relationships. His own new phylogenetic tables of the species of *Pinus* are based partly upon needle anatomy, including number of vascular bundles and position of resin canals, and upon size of pollen grains.

The genus is divided into 3 subgenera and 10 sections. Subgenus Ducampopinus contains the single species *Pinus krempfii* Lecomte of Vietnam, distinguished by 2 flattened needles. Subgenus Eupinus with 5 sections contains the hard pines and also 10 species of soft pines, including the pinyons. Subgenus Cembrapinus with 4 sections contains the 5-needle soft pines with 2 exceptions.

Species accepted in the genus *Pinus* total 122 (76 in the New World), far more than recognized by any previous author. In comparison Shaw (1914) admitted 66 species, Pilger (1926) 80-90, and Dallimore and Jackson (1948) 71. The additions include species described or elevated from varieties in recent years and similar new combinations proposed here. For example, South Florida slash pine becomes *Pinus densa*. Gaussen has not only accepted all of Martínez's Mexican segrepates but has raised 6 of the latter's varieties to specific rank. He explains that groups with different cone characters and geographic distribution have been separated as species.

The 45-page key to species ends in a botanical description of each accepted species or variety. The classification of species, or descriptive text, occupies 113 pages. Species descriptions, according to the author (p. 2), are compiled from other works but have been compared with trees in the Arboretum of Joué̇u. There are notes on size, bark, wood, distribution, and uses, especially in forestry. Current synonyms, common names, and varieties are mentioned. For each species there is a drawing of a cone, usually closed. Six plates of photographs illustrate large forest trees. The 35 pages on fossil pines contain a list of species and additional drawings of cones.

Gaussen states that he has retained scientific names used by non-specialists, such as foresters, horticulturists, and geographers to avoid changes in synonymy owing to the law of priority. Examples noted by the reviewer are *Pinus excelsa*, *P. longifolia*, and *P. parryana*. Incidentally, the new combinations are not validly published because citation of the basionym (epithet-bringing synonym) is omitted. Likewise, the 10 names proposed for the sections are illegitimate because Latin diagnoses are lacking, but older names are available for most of these sections.

Recent publications are cited by author and year, but no bibliography of references is provided in this separately published chapter.

This monograph will be a useful reference for foresters and botanists interested in exotic species of the genus *Pinus*, such as for introduction or hybridization in tree improvement programs. It is unlikely that the large number of species will be accepted by contemporary workers. Wide differences of opinion among different specialists in the classification indicate the desirability of additional evaluation of the different characters and especially more hybridization tests within this most important tree genus.

The Movement of Water in Trees

BY
THEODORE T. KOZLOWSKI

IT IS WELL KNOWN that large amounts of water are transported daily through individual trees (Kozlowski 1958). After soil water is absorbed through the roots it traverses several layers of root cells and then ascends in the xylem. The effective zone of water conduction in intact tree stems commonly consists of a cylinder located in the outer sapwood. However, the amount of cross-sectional area which is actually involved in water conduction varies in different species (Fig. 1). Whereas in ring-porous species water movement is generally confined to a thin cylinder of the outer sapwood, and often to the outermost annual ring, the path of ascent in diffuse-porous trees usually occupies a considerably greater portion of the sapwood (Kramer and Kozlowski 1960).

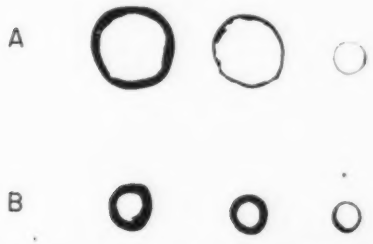

FIGURE 1. *Water conduction areas of stems of (A)* Ulmus americana *L. and (B)* Populus balsamifera *L. The paths of moisture movement were traced by injection of acid fuchsin dye into lower boles of standing trees. Following injection the trees were felled and sectioned and the staining patterns traced. The sections were taken at 3, 10, and 22 feet. Note the variations in percentage of cross sectional area involved in conduction in the two trees. (After Greenidge 1955a).*

Most of the water absorbed through roots moves upward through the stem, then into the branches, and is subsequently lost in foliar transpiration, but under certain conditions water moves laterally in trees and even downward. Quantitatively, however, upward movement exceeds any lateral movement or internal redistribution in intact trees. This paper deals with water transport and redistribution in trees with emphasis on the mechanism of upward transport.

Upward Movement

The mechanism whereby as much as a barrel of water ascends to the top of a transpiring tree in one day has intrigued foresters and plant physiologists for centuries. Over the years various theories were advanced to explain sap ascent. A number of the early theories, now long discarded, were reviewed by Copeland (1902). Some of these ascribed sap ascent to contraction of medullary rays, contractility of cell walls, agitation of trees by wind, and capillarity. Other theories receiving much more serious consideration over the years involved imbibition of water by cell walls and movement through cell walls, metabolic pumping of living cells, pushing of water up-

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ward by a hydrostatic pressure in the roots, and the pulling of water upward by transpiration.

Vital Theories

Several early investigators claimed that living cells were required for sap ascent. Despite a number of proponents (Godlewski 1884, Janse 1913, Bose 1923, Molisch 1929, and Handley 1939) vital theories have never received wide acceptance. Well before 1900 it was shown by Strasburger (1891, 1893) that trees cut at the base would take up a poisonous liquid which killed the living cells of the stem. That the same or another solution was then also drawn up the stem indicated that living cells were not required for ascent of sap. Strasburger (1891, 1893) and Overton (1911b) demonstrated with several species of trees that solutions of various poisons, including picric acid, carbolic acid, and copper sulfate, travelled to the tops of trees. Overton (1911a) concluded that withering of leaves on stems killed by heat was not due to lack of water but to toxic products which were transported to the leaves.

Bose (1923) believed that water was pumped upward by alternate contraction and expansion of living cortical cells. This theory was severely criticized by Shull (1923) and others. Benedict (1927), for example, tried to apply the Bose theory to ten species of trees and concluded that the actual rate of sap flow under maximum conditions of transpiration was from 8,000 to 30,000 times as rapid as would be possible under the Bose theory. In Strasburger's early experiments with poisons great care was taken to avoid introducing air blocks into stems. More drastic treatments were imposed by Scholander *et al.* (1955), who introduced air into stems and followed this with poison. A vine 13 m tall was cut off and allowed to absorb air through the cut surfaces for 20 minutes, until wilting occurred; then a 10 percent solution of copper sulfate was introduced. Even the combination of an air block and poison did not prevent ascent of fluid above atmospheric height and into the uppermost leaves. In another experiment the rate of water uptake was measured for 20 minutes and then water was replaced with 10 percent copper sulfate. The rate of uptake was not significantly reduced. Such observations strongly indicate that the mechanism of sap ascent does not involve metabolic sap pumps.

Root Pressure Theory

It often is claimed that root pressure may be a factor of some significance in ascent of sap (White 1938, White *et al.* 1958, Friesner 1940). However, it has been demonstrated repeatedly since 1900 that water ascends to tops of plants whose roots have been removed (Strasburger 1891, 1893; Scholander *et al.* 1957). If a hydrostatic pressure in roots was responsible for pushing water upward in the tallest trees, pressures approximating 10 atm. would be required at the base. Usually when holes are bored at the base of a tree which has already leafed out, sap flow does not occur but water poured into the hole is absorbed. This suggests that the pressure in the trunk is subatmospheric (Fisher 1949). Root pressure occurs in some species but not in others. Yet even those species which show root pressure fail to show it in significant amounts at the time of year when transpiration is greatest. Furthermore, root pressure does not develop in roots in cold or poorly aerated media or in dry soil (Kramer 1956).

It is widely held that root pressure is too weak a force to account for movement of water to tops of tall trees. Hales (1727) measured root pressures well under 2 atm. in grape, and pressures of up to 3.5 atm. have been reported for birch (Clark 1874, Merwin and Lyon 1909, Ingold 1935, Lundegardh 1954). White (1938) observed root pressure in excess of 6 atm. in excised tomato roots grown in culture solution, but practically all other measurements have given considerably lower values.

The volume of liquid exuded by stumps of "detopped" plants is only a small frac-

tion of the amount absorbed by freely transpiring plants (Kramer 1939, Army and Kozlowski 1951). It has been argued that lack of root pressure when tops are cut off is not adequate proof that root pressure does not occur in intact, freely transpiring plants. However, as Kramer (1956) points out, it does not seem likely that top removal will shock plants and stop root pressure because exudation does occur immediately from stumps when plants growing in moist soil and a humid atmosphere have their tops severed. Still another argument against the importance of root pressure to sap ascent is that freely transpiring plants absorb water against much greater diffusion pressure deficits than do detopped root systems (Army and Kozlowski 1951). For these reasons root pressure is generally considered not to play a primary role in ascent of sap.

Cohesion of Water Theory

The cohesion theory proposes that water loss from the leaves sets in motion the ascent of sap and that water moves through plants because of its continuity and cohesion. Requirements for the cohesion theory include high cohesive forces of water confined in tubes of small diameter, a continuous water system throughout the plant protected from air entry, and a free energy gradient resulting from evaporation of water. According to this theory evaporation of water from leaf cell walls causes high diffusion pressure deficits to develop in the cell walls which in turn motivate water movement into evaporating cells from neighboring cells and eventually from xylem elements. As pressure on water in non-living xylem elements is reduced, the diffusion pressure deficit of this water is increased and a gradient results, from the leaves downward, along which water moves. Rapid water loss at the top of the plant reduces the pressure sufficiently to cause tension.

In connection with the cohesion theory it often is stated that "transpiration pull" initiates ascent of sap by way of diffusion of liquid water from the tops of vessels in leaves to evaporating mesophyll cell walls. However, Levitt (1956) argues that this is impossible because the diffusion rate of water vapor is many times faster than that of liquid water. According to Levitt water is actually supplied to the evaporating mesophyll cells by mass movement of a cohesive liquid column. His view is that imbibitional forces are increased at the surface because of evaporation and this causes mass movement of water from the soil through the whole plant.

Of the several theories advanced to explain the mechanism of ascent of sap the most commonly accepted is the cohesion theory. Since the basic theory was advanced in 1894 by Dixon and Joly and supported by Askenasy (1895) it has been extended and widely supported (Dixon 1897, 1907, 1914, 1924; Renner 1915; Bode 1923; Smith *et al.* 1931; Thut 1932; Gibbs 1935; Kramer 1939, 1949; Strugger 1943; Stocking 1945; Crafts *et al.* 1949; Curtis and Clark 1951; Meyer 1952; Bonner and Galston 1952; Levitt 1956). The theory has also had its critics. Priestley (1935) for example, believed that the theory did not rest on a satisfactory experimental basis. He stated that he could find no good evidence of the existence of high tensions in continuous liquid columns. Preston (1938, 1952, 1958) presented evidence that considerable gas is present in wood which he believes is a great threat to the maintenance of moving columns of water. In addition he suggested that the tensile strength of water in a tree may be less than 30 atm. This, Preston concludes, renders probable the fracture of water columns.

During recent years the cohesion theory has been reexamined and reevaluated in the light of new data. Several questions have been raised and possible objections advanced (Greenidge 1954, 1955a, 1955b, 1957; Scholander 1958; Scholander *et al.* 1955, 1957; Preston 1958; Lundegardh

1954; White *et al.* 1958). These objections include the impossibility of existence of tensive channels in presence of free air bubbles, inadequacy of tensile strength of water, failure of stem pressures to decrease proportionally with increase in height, and insufficient evidence of the existence of continuous water columns. Unequivocal acceptance of the cohesion theory must eventually provide experimental evidence that the objections do not invalidate the theory. These objections will be reviewed briefly.

Tensions. Evidence for cohesive tensions in freely transpiring plants comes from a variety of observations. A leafy twig cut under water and sealed to the top of a mercury manometer has been shown to pull mercury above barometric levels (Thut 1932). Shoots also pull water through an artificially imposed resistance faster than can be demonstrated with a vacuum pump (Renner 1911, 1915). Such a method does not show whether a precise hydrostatic gradient exists with height increase, but it does demonstrate cohesive tensions (Scholander 1958). Tensions were demonstrated by McDermott (1941) in still another way. If water in a vessel is under tension puncturing the vessel will cause the water column to snap apart. However, if a twig segment were cut at two ends simultaneously there should be less probability of water removal from the segment, because tensions would presumably be released at both ends at the same time. If both ends are not cut simultaneously the amount of water removed from a branch segment should be proportional to the amount of tension and the time interval between cutting of the two ends. Using two cutters McDermott made a snap cut, instantaneously, on each side of a twig segment, so that there would be no chance for the water to snap apart and be pulled from the segment. Under conditions favoring high transpiration he found higher water contents in segments cut in this manner than in segments taken by cutting a whole twig and then cutting a sample out of it. Gibbs (1942) made similar experiments and fully substantiated McDermott's demonstration of tensions in trees.

Other evidence for existence of tensions comes from observed decreases in diameters of tree stems when transpiration is high. If water is under tension, the strain in the vessels causes their diameters to decrease. Bode (1923) observed that when cut ends of shoots were plugged the decrease in diameter of the twig and individual vessels was greater than could be caused by a vacuum pump. Dendrographic measurements of tree trunks show that stems decrease in diameter during the day and increase at night, when tension presumably is released (MacDougal 1925, 1938; Gibbs 1935). Fritts (1958) reported that in late May and early June diameter growth of American beech (*Fagus grandifolia* Ehrh.) was fairly steady with very slight shrinkage during midday. In early July when temperatures and transpiration were higher reversible variations in diameter became more marked. With decreasing soil moisture and clearing weather, midday shrinkage increased in amount. Crafts (1939) demonstrated tension by noting that jarring or flattening of intact xylem elements caused cohesive sap columns to break and retreat rapidly.

Continuity of water columns. As early as 1902 Copeland argued that chains of bubbles in xylem would not allow for tensile columns of water. Peirce (1934) questioned that continuous liquid columns of water were present during high transpiration. He suggested that water existed in conducting elements in the form of hollow cylinders with water vapor within the cylinder. Preston (1938) also concluded that many vessels were filled with gas. Crafts *et al.* (1949) stated that Preston's data (his work involved use of dyes) did not prove that vessels in the intact trunk contained gas. Moreover, they argue that when tensions in the xylem are very high it is doubtful if injection can be accomplished without some vapor bubble forma-

tion. More recently Preston (1958) acknowledged that some continuous columns must be present because it is not possible to explain water movement at the necessary rate in the vapor phase. Preston stated that the issue is not whether continuous columns exist but how many are required and where they exist. Again the presence of gas was cited as a threat to continuity of water columns. In addition he pointed out that any water columns present end in slender twigs which are tossed about in the wind. For such reasons he felt that water columns under tension were short-lived.

On the other hand the existence of continuous columns of water has been acknowledged by a number of investigators (Bode 1923, Holle 1915, Gibbs 1935, Lundegardh 1954, Scholander *et al.* 1955, and Scholander 1958). Bode (1923) and Holle (1915) reported that they observed continuous columns of water in vessels. Although Bode recognized that some vessels contained gas he considered the conducting ones to be full of water. Crafts (1939) reported that the bark of *Ribes* plants in a state of permanent wilting could be removed without breaking the water columns in the vessels. A slight jarring of the vessels with the back of a scalpel caused vapor to form and the water columns to recede so rapidly that they could not be followed. Crafts was able to produce bubbles that expanded slowly or rapidly in plants with lower water deficits. In plants with negligible water deficits he produced bubbles that gradually disappeared. He stated that the formation of vapor bubbles in uncut vessels and their continued expansion after they formed proved the existence of tensions because the vapor phase could not continue to expand if the pressure exceeded that of saturated water vapor at the temperature of the experiment. The very rapid expansion of bubbles in vessels of permanently wilted plants indicated high tension, for in expansion the water that was originally present had to move out rapidly to overcome inertia and resistance in order to flow through capillaries.

Lundegardh (1954) acknowledged that "fast mobile water" formed continuous columns from roots to leaves, presumably in the medium sized elements. In dealing with the question of whether or not a low tension gas phase coexists with sap in vessels Scholander *et al.* (1955) compared gaseous nitrogen contents of sap at various stem heights and times. Sections of stems or branches of vines were cut out and sap collected from the lower end under paraffin oil. The sap flowed out under the oil and there was no evidence of gas bubbles even when twigs were taken from the upper parts of the plant during times of rapid transpiration. The quantity of nitrogen gas dissolved in the sap at various heights was similar to that of air-equilibrated water. No appreciable extraction occurred during ascent. Scholander *et al.* (1955) concluded that the elements which conducted water were completely filled with sap and were protected from entrance of gas by diffusion from gas-filled vessels. Furthermore the vessels in small branches high up on the stems apparently contained an abundance of sap during times of rapid transpiration.

Air blocks. It is well known that tree stems contain considerable air (Chase 1934, Lundegardh 1954). Haines (1935) reported that although he found no air present in early spring before bud expansion he found considerable air in conducting elements after buds opened. It has been argued that air in conducting elements eliminates them from the system of water movement. Such breaks in the vascular system could be repaired by high root pressures but these appear to be inadequate in most species. In recent years the work of Scholander and his colleagues has done much to evaluate the speculation about air blockage as a threat to the cohesion theory. Some of their experiments deserve brief review.

Scholander *et al.* (1955) tested the effects of air embolism on the rate of water uptake in tall grape vines. Two leafy

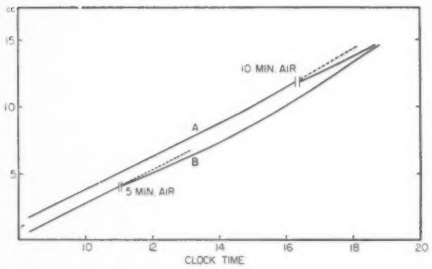

FIGURE 2. *Rates of water uptake of two detached grapevine branches. The vines were given air instead of water at the time indicated by the double vertical lines. (Redrawn from Scholander* et al. *1955).*

branches were cut under water and their bases immersed in a water reservoir. One plant was given a 5 min. air embolus by lowering the reservoir. There was a slight drop in the rate of water uptake but this was soon overcome. The other branch received a 10 min. embolus and it too had a slightly depressed rate but it almost recovered its original rate when the experiment was terminated (Fig. 2).

In another experiment a cut vine was placed in a water reservoir. At noon it was given 6 min. of air. Presumably every water column receded up the stem and was followed by air. The air emboli in this vine, after 5 min. of aspirated air, were estimated as originally a meter or two long. However, the rate of water uptake was undiminished when the vine was reimmersed in the water reservoir. Another vine, given a 6 min. helium embolus, had a rate of water uptake after it aspirated air essentially that of the vine without the air embolism.

In still another experiment conducted on a hot sunny day tall vines were cut off with a machete, recut in air, and then placed in a water reservoir. Thus an air embolism was introduced. The next day vines were given 30 min. of air. Under this treatment wilting occurred after about 30 min. But even this drastic treatment did not stop water uptake when the vines were replaced in a water reservoir. Turgidity was regained within 20 min. to an hour. During the next 4 days transpiration continued, at a lowered rate in these vines which had severe air blockage.

Still another line of investigation has been pursued to evaluate the importance of air blocks in water movement. Tree trunks were cut on opposite sides at different levels so presumably continuous water columns were severed. The failure of wilting to follow as a consequence of such saw cuts was cited as evidence at variance with the cohesion theory (Preston 1952; Greenidge 1955b, 1957). Elazari-Volcani (1936) observed that citrus trees did not wilt when their trunks were deeply cut from opposite sides and Greenidge (1955b) observed that dye solutions moved up to horizontal saw cuts in tree stems and then were transferred laterally into regions above the incisions. Postlethwait and Rogers (1958) used radioactive iodine and phosphorous to trace the transpiration stream in hickory (*Carya* spp.), red pine (*Pinus resinosa* Ait.), and American hornbeam (*Carpinus caroliniana* Walt.) trees with variously oriented, overlapping horizontal saw cuts at different stem heights. The isotopes moved up control trees in straight lines. However, in trees with horizontal stem cuts the isotopes moved vertically up to a cut and then readily passed around the cut. Thereafter movement was vertical until another cut was encountered. The path of the transpiration stream was made to move from one side of the tree to the other by properly distributed cuts. Opposing cuts only 6 in. apart failed to block the transpiration stream (Fig. 3).

Scholander *et al.* (1957) made double horizontal saw cuts in *Tetracera* vines and found that only those vessels severed by the cut became inoperative in water transport. Above and below this the vessels contained water and conduction was unimpaired. They concluded that plants failed to wilt because the transpiration stream had ade-

quate force to overcome the increased resistance to water movement by developing a greater pressure gradient across the region of non-functioning vessels (Fig. 4). By demonstrating that the introduced air was confined to the severed vessels and tracheids and did not spread into other elements through pits or micropores in walls Scholander *et al.* (1957) verified experimentally an assumption made by Dixon in 1914. Apparently the air breaks did not jeopardize the total cohesive system. These experiments were interpreted as removing one of the most serious criticisms of the cohesion theory (Scholander 1958). From such experiments one may deduce that upward water movement tends to follow a path of least resistance, hence water tends to move in vessels. If these are blocked, by cuts or tyloses for example, water must move through shorter elements where it encounters greater resistance, as Scholander (1958) has demonstrated. Thus in trees with horizontal saw cuts tracheids and fibers appear to be involved in water transport.

Air blockage undoubtedly occurs when sap freezes during the winter for the dis-

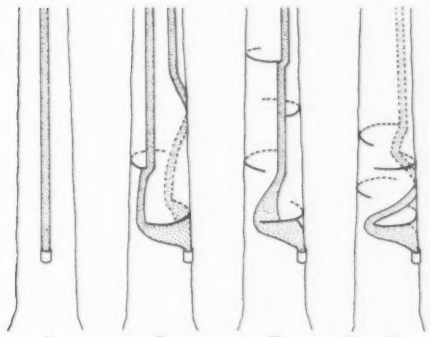

FIGURE 3. *The course of movement of* P^{32} *around cuts in* Pinus resinosa *stems. The location of the isotope is indicated by the stippled area. With no horizontal cuts present (Tree 1) the isotope moved vertically. With 2 opposite cuts (Tree 2) the isotope moved around the cuts and then vertically. With 4 cuts (Tree 3) the isotope moved around the first cut and then vertically with only enough curving to get around the cuts. With 4 cuts differently oriented and only 6 inches apart (Tree 4) the isotope moved and spiralled around the cuts in its ascent. (Redrawn from Postlethwait and Rogers 1958).*

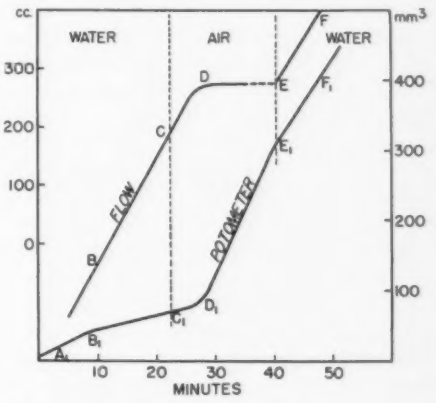

FIGURE 4. *Measurements of the amount of water and air taken in by a cut vine given a water-air-water sequence through the base of the stem (upper curve). Simultaneous measurements of the pressure in microporous structures as indicated by infiltration from a potometer attached to the stem are also shown. (Lower curve).*

When the vine was cut under water at B_1 *the potometer rate was reduced (from* A_1 B_1 *to* B_1 C_1*). At* CC_1 *the stump was supplied with air instead of water. The rate of air uptake by the stump was the same for a few minutes as the previous rate of water uptake (B C D). However, the rate of air uptake soon stopped (D) while the potometer rate increased greatly (*D_1 E_1*), indicating a large pressure drop.*

When the stump was again given water at EE_1 *the rate of water uptake was the same as it was before the air block (EF) but the potometer rate (*E_1 F_1*) was higher than before the air block (*B_1 C_1*). Since water uptake was not decreased despite air-blocked vessels the rate of movement through micropores must have increased. (Redrawn from Scholander* et al. *1957).*

solved gas is forced out as bubbles. Lybeck (1960) found that small trees at all levels were frozen during the winter and were not supercooled. Gas evolution by freezing is not evenly distributed for Lybeck (1960) observed that some tracheids in spruce did not contain bubbles after thawing. She concluded that some diffusion took place through the walls. When a bubble forms there will be a diffusion of dissolved gas into the low pressure gas phase from adjoining tracheids. Lybeck believes that movement of gases probably does not occur over large distances because supercooling precedes freezing which occurs evenly and rapidly. At present it has not been clearly demonstrated that there is a mechanism that can rapidly redissolve air bubbles which presumably seed the vascular system in winter.

Although it is undoubtedly true that wood contains considerable gas especially in summer, trees apparently have more than enough conducting tissue to supply their tops with water and only some of the elements function as water conductors. The work of Scholander and his colleagues indicates that air bubbles remain confined to certain vessels and do not necessarily interfere with liquid continuity and cohesion in other vessels.

Hydrostatic gradients. If the cohesion theory is correct trees should show a precise hydrostatic gradient with increase in height. The pressure should decrease one atm. for every 10 m increase in height. Scholander *et al.* (1955) attempted to measure such pressures using a manometer clamped pressure and vacuum tight to grape vines. When measurements were taken in the spring before the leaves were out the sap pressure was adequate to lift sap higher than the top of the vine. The pressure decreased precisely (1 atm. per 10 m in height) indicating a pressure continuum through the vine. However, when the leaves were out these precise gradients were not always found, and in fact, in the daytime when transpiration occurred the data were erratic. Pressures at the base were low and they were usually higher at the top. Such an inverse gradient does not support the cohesion theory.

Scholander *et al.* (1955) point out that the technique of measurement may have shortcomings and they did not exclude the possibility that cohesive sap tensions existed during high transpiration. In support of their suspicion that the pressures recorded during high transpiration rates may not have been accurate was the fact that they could easily obtain sap through the manometer punch during the night, but they could not do so during the day. Scholander *et al.* (1957) also failed to find accurate positive hydrostatic gradients in *Tetracera* vines during transpiration. However, they expected such gradients to be found when proper techniques are worked out.

Tensile strength of water. Over the years there has been a lively controversy about whether or not the tensile strength of water is adequate to support the cohesion theory. Greenidge (1954) called attention to the possibility of widespread rupture of stretched water columns under conditons favoring high transpiration and low absorption.

For water at ordinary temperatures the fracture pressure may be calculated to be 1300 negative atmospheres. When the fracture pressure is measured, however, values ranging from positive vapor pressure to negative pressures of about 350 atm. have been reported. Thus experimentally water has withstood up to about 30 percent of the theoretical value. Reported observations of tensile strengths of water differ greatly with the method of its determination. Dixon (1914), Ursprung (1915), and Renner (1915) obtained values, variously determined, of at least 200 atm. Budgett (1912), Temperley and Chambers (1946), Temperley (1946), Scott *et al.* (1948), and Vincent and Simmonds (1943) give much lower values. Greenidge (1957) cites several other investigators who reported a wide scatter of values. It has even been reported by Silver (1942)

that the tensile stress which can be maintained by water is negligible because of the existence of evaporation nuclei.

Many of the determinations of tensile strength were made by the Berthelot method. This involves filling a capillary tube with water and sealing it to leave only a small vapor bubble and possibly air. The liquid in the tube is expanded by heating until it fills the tube completely. Then it is cooled until the liquid column fractures. Tension existing in the liquid is calculated from the computed volume of the extension and the compressibility coefficient of the liquid. Scott *et al.* (1948) concluded that the high values often reported were due to traces of air ordinarily present in Berthelot tubes. They prepared tubes in an evacuated system, using water from which air had been removed. Measurements with air-free tubes indicated that 32 atm. was the average maximum tension that water could withstand. Fisher (1949) believes that the low experimental values suggest that the initial vapor bubbles form at the interface between the water and container, whereas theoretical fracture pressures are obtained by assuming that the vapor bubble causing fracture forms in the interior of the liquid. Tiny cracks or irregularities in glass containers probably account for the wide variations in observed fractured pressures.

Preston (1958), citing Temperley (1947) and Temperley and Chambers (1946), concluded that the tensile strength of water may be below 30 atm. and this would place the cohesion theory on uncertain ground. With an improved method using tubes open at both ends Briggs (1950) measured the limiting negative pressure of water over a temperature range of 0° to 50° C. He obtained values up to 280 atm. The negative pressure was greatest (app. 280 atm.) around 20° C and decreased to approximately 210 atm. at 50° C. However, between 5° C and 0° C the limiting negative pressure underwent a marked change, dropping to about 20 atm.

This method, which affords high reproducibility, did not indicate whether fracture originated in the wall of the vessel or in the body of the liquid. It demonstrates fracture which might be caused by loss of adhesion, or loss of cohesion. Despite the range of experimental values reported for the tensile strength of water the work of Fisher (1949) appears to account for much of the scatter of values obtained, and supports the cohesion theory. Fisher believes that the tensile strength of water in plants is completely adequate for the requirements of the cohesion theory. He adds[1] that he would expect the strength to be higher in plants than in glass tubes because of a strong water-wall interface. Furthermore, he suggests that water diffusion into plants through cell walls will tend to suppress the presence of small gas bubbles that would tend to reduce the strength. Actually only about 20 atmospheres of tension are required in a tree 300 feet high and this value is well within the forces observed with improved techniques. Briggs[2] also believes that the tensile strength of water is amply sufficient to support the cohesion theory.

Present status of the cohesion theory. Critical research of the last decade has in general refuted some of the most serious arguments against the cohesion theory. Scholander and his colleagues have provided evidence of continuous, freely mobile sap columns and absence of metabolic pumps. Furthermore, they have shown that even severe air blockage does not jeopardize a total cohesive system. Trees appear to have sufficient crown and adequate conducting system to provide for lateral movement of water around confined air blockages. Actually, not much conducting system is required. Considerable gas is present in stems but this does not appear to constitute a serious objection to the cohesion theory as has been often supposed. Even when water columns break there apparently are enough

[1]Private communication, J. C. Fisher, 1959.
[2]Private communication, L. J. Briggs, 1959.

intact columns to make sap ascent possible.

The work of Fisher and Briggs on tensile strength of water suggests that many of the low values reported are traceable to methodology. The cohesion theory would be jeopardized only if under the best conditions the tensile strength of water were less than 20 atm. Recent evidence based on improved methodology suggests that the tensile strength of water is sufficiently high to permit operation of the cohesion theory.

Some criticisms of the cohesion theory are still valid. There is lack of a demonstrated mechanism for dissipating air seeding as a result of freezing in twigs and lack of a demonstrated precise hydrostatic gradient with height. Unequivocal acceptance of the cohesion theory requires clarification of these issues and more research is obviously necessary. Nevertheless, recent research is interpreted as providing the cohesion theory with substantial net reinforcement. The present state of knowledge of the sap ascent mechanism was perhaps aptly summarized by Scholander (1958): "The cohesion theory is very likely the correct explanation for the phenomenon, but in crucial points it still lacks experimental evidence."

Internal Redistribution

Lateral transfer of water has been observed in both intact and injured trees. Upward transport through stems may occur vertically or there may be considerable deviation from a strictly vertical path. Different patterns of upward water conduction often are traceable to anatomical differences in xylem structure. Rudinsky and Vité (1959) found five distinct water conducting patterns in conifers. These included:

1. Spiral ascent, turning right. Water ascended in a spiral band that ran from the outermost growth ring clockwise toward the stem center.

2. Spiral ascent, turning left. Water ascended in a spiral band which ran counter-clockwise from the periphery toward the stem center.

3. Interlocked ascent. Water ascended in a zigzag pattern.

4. Sectorial, winding ascent. Water ascended in a sector which tended to wind around the tree.

5. Sectorial, straight ascent. Water ascended in a vertical sector.

Rudinsky and Vité observed that closely related species always exhibited the same water conduction pattern and this was also true for related genera. However, differences often occurred within a family. In Pinaceae, for example, at least three distinct water conducting systems were observed.

Greenidge (1955a) demonstrated lateral transfer in deciduous trees also by injecting acid fuchsin at various points on tree stems and later observing the staining pattern in cross sections taken at various heights. The rate and amount of lateral transfer varied considerably with species. Lateral transfer was most apparent in yellow birch and beech and less pronounced in elm. Lateral transport ultimately caused a complete ring of stained wood. Preston (1952) and Postlethwait and Rogers (1958) have also demonstrated lateral transfer in cut stems.

When roots were removed from one side of a tree the total amount of moisture taken up by the tree was reduced but there were no significant differences in moisture content between the sides with and those without roots (Auchter 1923). Furr and Taylor (1933) removed roots on various sides of 30-year-old lemon trees and then studied their fruit volumes. The position of the fruit relative to cut or uncut roots did not affect changes in fruit volume, indicating a ready lateral translocation of water throughout injured trees. When irrigation was applied on alternate sides of trees on successive irrigation dates internal redistribution of water was readily accomplished.

There is also ample evidence of internal redistribution of water in intact trees. For example, during the afternoon of a hot,

dry day, lemons which remain attached to trees decrease in diameter and become comparatively soft but they recover turgidity at night. The loss of water by transpiration from the leaves apparently sets up a gradient toward the leaves and water is extracted from the fruits by the leaves. The amount of water withdrawn from fruits depends on the amount of available soil moisture. According to Bartholomew (1926) the drier the soil the greater the amount of water extracted from the fruit and the more prolonged the water deficit. The transfer of water from apples, oranges, cherries, plums, and walnuts to leaves also has been reported (Magness *et al.* 1935, Chandler 1914, MacDougal 1924, Coit and Hodson 1919, Rokach 1953). Such movement apparently occurs over a considerable distance. Rokach (1953) reported that water was easily transported from an orange to a defoliated main branch to a leafy lateral branch. Coit and Hodgson (1919) attributed a decrease of 25 to 35 percent in moisture content of oranges during hot and dry weather to leaf suction.

There also are diurnal variations in moisture contents of dormant buds. Their low moisture contents in midday are caused by bud transpiration and probably also as a result of some internal redistribution of moisture (Kozlowski and Petersen 1960). Under conditions of internal water deficiency actively meristematic tissues such as growing stem and root tips and growing fruits apparently develop higher diffusion pressure deficits than other tissues from which they draw water. The high diffusion pressure deficits of such tissues are largely of imbibitional origin (Meyer 1956). Haasis (1932) observed that a small tree 1 m high was shrinking in diameter during 9 weeks in March, April, May, but its terminal shoot continued to elongate. He concluded that water was drawn from one part of the tree and used to maintain turgidity of cells in another part. Another example of internal redistribution is the observation that older leaves are the first to wilt when soil moisture deficits occur (Delf 1912, Bakke 1918, Kramer 1949).

Downward Movement

There are many reports of dew absorption by plants in dry soil, subsequent downward transport, and release of moisture into dry soil through the root system (Magistad and Breazeale 1929, Breazeale 1930, Breazeale and Crider 1934, Breazeale *et al.* 1950, Wadsworth 1933). Brierley (1936) observed that when water was sprayed on leaves of one of two wilted raspberry canes both canes became turgid. Arvidson (1951) concluded that during droughts many trees in Sweden utilized moisture absorbed from the air. Whether significant downward transport of water occurs has been questioned by several investigators (Hendrickson and Veihmeyer 1931, James 1954). Stone and Fowells (1955), Stone *et al.* (1950, 1956), and Stone (1957, 1958), supplied artificial dew to conifers whose roots were sealed in soil or in flasks. Water was absorbed and moved back through the plant and out through the roots into the empty flasks only when the temperature in the flasks fluctuated and the relative humidity in the flasks decreased. Leaves of plants rooted in soil absorbed water but downward movement of water into the soil was not demonstrated. Survival of pine seedlings in soil at the wilting percentage was attributed to resaturation of needles by dew and a reduction in amount of water removed from the root system. Bormann (1957) used a technique in which two root systems were developed on one plant. One of these two root systems was planted with another plant in one pot, and the other root system in another pot. When water was added only to the pot containing the single root system, sufficient water was moved to the other plant to maintain it for some time.

Slatyer (1956) demonstrated movement of moisture in shortleaf pine seedlings both upward and downward under laboratory conditions, depending on the dif-

fusion pressure gradient. He also showed that moisture was absorbed from an unsaturated atmosphere as long as there was a favorable gradient. He suggested that in arid regions where humidity is high at night and the diffusion pressure deficit of soil moisture may reach several hundred atmospheres (Alway *et al.* 1919) water might move downward through the plant and possibly into the soil. In another study Slatyer (1957) observed that at a high total soil moisture stress water was absorbed from the air and accumulated in shoots. Although a diffusion gradient existed which favored movement of water downward through the plant and into the soil, no evidence of actual movement into the soil was found, presumably because of a discontinuity of contact between roots and soil. Thus although there is some disagreement as to whether or not plants actually "pump" water downward into dry soil, it is generally agreed that plants in very dry soil can absorb water from a moist atmosphere. The absorbed water moves downward to some extent and at least accumulates in the plant.

In trees bound together by root grafts there undoubtedly is considerable water movement in roots in a direction away from the tops of some grafted trees. Kuntz and Riker (1955) demonstrated that in relatively dense stands of northern pin oaks (*Quercus ellipsoidalis* E. J. Hill) in central Wisconsin practically all trees were united to neighboring trees through root grafts. When dominant and suppressed trees were connected by root grafts, movements of moisture occurred in both directions, but most often it occurred from the dominant to the suppressed trees. This may assist survival of suppressed trees. Very little work has been done in evaluating the water economy of trees joined by root grafts. The possibility of trees serving as water reservoirs for trees grafted to them involves intriguing ecological implications which need to be examined further.

Summary

1. Upward movement, internal redistribution and downward movement of water in trees are reviewed.

2. The vital, root pressure and cohesion of water theories of sap ascent are characterized. Recently cited objections to the cohesion theory include impossibility of maintaining tensions in presence of air in stems, inadequacy of tensile strength of water, failure of stem pressures to increase proportionally with height, and inadequacy of evidence for existence of continuous water columns. These objectives are evaluated.

3. Critical research of the last decade has provided the cohesion theory with considerable reinforcement, but some criticisms of the theory appear to be valid.

4. Evidence for internal redistribution of water in trees is presented.

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Literature Cited: Designate references to literature citations by the author's name and year of publication inserted in parentheses at the appropriate place in the text. If there are more than two authors, list only the senior author's name in the text with the abbreviation *et al.* Example: (Smith *et al.* 1954). Only published references should be given in *Literature Cited*. Periodical abbreviations should follow *Guide to the use of Forestry Abstracts*, Commonwealth Forestry Bureau, Oxford, England, 1950.

Nomenclature and Terminology: When a species is first mentioned in a paper, its common name must be immediately followed by its italicized scientific name, with authority abbreviation, in parentheses. The authority for nomenclature of North American tree species is *Check List of Native and Naturalized Trees of the United States*, Agriculture Handbook 41, Forest Service, U. S. Dept. Agric. Washington, D. C., 1953. Authorities for nomenclature of other plants and of animals are listed in the *Style Manual for Biological Journals*. Technical usage in forestry and allied fields follows *Forestry Terminology*, 3rd Edition, Society of American Foresters, Washington 6, D. C. 1958.